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The dendrochronological statistic mean sensitivity quantifies the environmental stress experienced by trees; however, researchers have not applied mean sensitivity to interpretations of macroclimatic tolerance, because, in the southwestern United States, where the metric was developed, species' discontinuous distributions on mountains obscure range-wide patterns, and because topoedaphic factors disproportionately influence mean sensitivity in these semi-arid environments. In this thesis, I examine geospatial patterns of mean sensitivity in temperate, humid regions, specifically for *Pinus strobus*.

I developed *P. strobus* chronologies for sites across an elevation gradient in North Carolina. Correlation analyses of topography and individual tree data reveal that no topographic factor influences mean sensitivity. Conversely, broad-scale trends are evident in a collection of range-wide chronologies; specifically, mean sensitivity is lowest in the range core and increases toward range margins. These results suggest that mean sensitivity can be interpreted to reflect macroclimatic suitability. Such interpretation facilitates the identification of populations that are poorly adapted to their climatic conditions. Further, geographically weighted regression of mean sensitivity allows one to determine the specific climatic component that precludes complacent growth at any location. By accounting for non-stationarity, geographically weighted regression could even identify ecotypic responses.

Applying these methods to *Pinus strobus* helped to identify the species' western populations as the most sensitive, due to moisture stress. Results indicate that the high-elevation, southern populations are the least sensitive, due to abundant moisture. The geographically weighted regression only elucidated the quadratic relationship between mean sensitivity and climate, while ecotypic responses were not evident with such sparse data.

GEOSPATIAL ANALYSIS OF MEAN SENSITIVITY IN PINUS STROBUS

by

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TABLE OF CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

Page

CHAPTER I

INTRODUCTION

Forest composition and structure are projected to experience rapid modification in the coming decades as a result of climate change (Bachelet et al., 2001; Lasch et al., 2002; Crawford, 2008). Fragile ecosystems will be lost as species' ranges contract, expand, and shift (Iverson et al., 2001; Lawler et al., 2006; Prasad et al., 2007). In fact, this is already taking place. Danby and Hik (2007) have documented a 65 to 85 m rise of *Picea glauca* treeline in the St. Elias Mountains. Lescop-Sinclair and Payette (1995) found that *Picea mariana* has moved 12 km closer to Hudson Bay since the late 1800s. As the most comprehensive evidence, meta-analyses by Parmesan and Yohe (2003), Hickling et al. (2006), and Thomas (2010) indicate that a majority of observed species have expanded their ranges poleward in response to climate change.

In addition to changes in species distributions, community structure will be altered as species' reproductive and growth trends adapt to new patterns of resource allocation. This, too, is already evident (Briffa et al., 1998a, 1998b; Soulé and Knapp, 2006; D'Arrigo et al., 2008). Higher levels of CO_2 are encouraging pollen production in younger and smaller specimens of *Pinus taeda* (Ladeau and Clark, 2006). *Pinus longaeva* near the upper treeline has responded to increased temperatures with increases in radial growth rates (Salzer et al. 2009). Jump et al. (2006) have documented a decline

in radial increment at the southern, low-elevation limit of *Fagus sylvatica*, with no corresponding decline at higher latitudes or elevations.

Traditionally, researchers have used the simplistic bioclimatic envelope model for interpreting current distributions and for predicting those of the future (Sykes et al., 1996; Shafer et al., 2001; Segurado and Araújo, 2004; Rehfeldt et al., 2006; Prasad et al., 2007). Such models are often derived from simple, binary, presence/absence data and operate under the flawed assumptions that climatic tolerance is consistent across a species' range (Pearson and Dawson, 2003, 2004; Murphy and Lovett-Doust, 2007) and that current distribution represents the fundamental niche of the species (Araújo and Pearson, 2005). Reality is much more problematic, due to intraspecific genetic variation (Stern and Roche, 1974; Epperson, 2003), interspecific competition (Woodward, 1987; Loehle, 1998), and geologic or climatic history (Hengeveld, 1990; Cox and Moore, 2003).

Ascertaining the complexities of a species' climatic tolerance is the critical first step in predicting future distributions and community structures (Biondi, 1999; Cook et al., 2001; Zhang and Hebda, 2004; Bhuta et al., 2009). For example, ecological models as well as growth/yield models can be improved with the implementation of parameters that account for climatic growth response and for spatial variation of the same (Cook and Cole, 1991; Graumlich, 1989; Mäkinen et al., 2001; Chhin et al., 2004). With knowledge of distinct climatic responses, it may even be possible to mitigate the effects of climate change (Newton, 2007; Goldblum, 2009). Since species often exhibit clinal and ecotypic variation across their ranges (Turesson, 1923; Langlet, 1934, 1963; Stern and Roche, 1974; Hengeveld, 1990), controlled seeding with selected genotypes may be employed to

stabilize forest composition and to maintain ecosystem balance (Ledig and Kitzmiller, 1992; Demeritt and Garrett, 1996; Morgenstern, 1996; Zhang and Hebda, 2004; Crawford, 2008; Chen et al., 2010).

Marginal and disjunct specimens hold the most promise as indicators of climatic constraints and as potentially valuable seed sources (Cook, 1961; Stern and Roche, 1974; Andreu et al., 2007). Their presence at the periphery suggests that they may have evolved an environmental tolerance that is unique to the species, making them better adapted to comparatively harsh conditions (Major and Bamberg, 1963; Stern and Roche, 1974; Crawford, 2008; Chen et al., 2010). Conversely, Kirkpatrick and Barton (1997) counter this assertion, arguing that genetic regression impedes adaptation to local conditions, as genes from the population core flow outward to the periphery (see also: Mayr, 1963; Morgenstern, 1996; Lenormand, 2002; Gaston, 2003). However, genetically-isolated, disjunct populations would not suffer this same genetic homogenization (Gaston, 2009). Small, disjunct populations may instead be maladapted as a result of genetic drift (Stern and Roche, 1974; Cox and Moore, 2000). Still, despite the threat of genetic drift, some isolated populations have persisted since the end of the Pleistocene (Radford, 1959; Hardin and Cooper, 1967; Cox and Moore, 2000), weathering the climatic vagaries of the Younger Dryas and hypsithermal periods as well as human-induced stresses, indicating that they have sufficient adaptive capacity. Such unique tolerances could, perhaps, signify incipient speciation (Stern and Roche, 1974). Empirical analysis is required to understand how these conflicting processes impact climatic tolerance across a species' range.

Provenance studies—in which a series of climatically distinct sites are established, and seeds from across a species' range are grown at each site for direct comparison—have long been the most effective means of identifying intraspecific, genetic variation (Morgenstern, 1996). However, for the purpose of understanding how that variation manifests through heterogeneous climatic responses, dendrochronology is more informative and can provide data at higher spatial and temporal resolutions (cf. Biondi, 1999). In contrast with provenance studies, dendrochronological analysis can be performed on specimens that live in natural, competitive environments, thereby revealing a more realistic response with practical implications.

Researchers have long asserted that a species' optimal climate is found near the center of its geographic distribution (Fritts, 1976; Hengeveld, 1990; Hart et al., 2010). Reciprocally, toward range margins, specimens should become increasingly limited by climate (Crawford, 2008). Such spatial patterns should be evinced in the dendrochronological record (Fritts, 1976; Fritts and Swetnam, 1989; Speer, 2010), particularly in values of mean sensitivity, which is a metric that quantifies interannual variability in ring-widths and can serve as a measure of climatic marginality (Fritts, 1976). Analysis of mean sensitivity across the range of a species may reveal a more nuanced climatic tolerance than is suggested by mere presence/absence data; it may even indicate which populations are best adapted to their local conditions and which are most vulnerable to climatic change.

Eastern white pine (*Pinus strobus* L.), an ecologically and economically valuable tree (Smith, 1995; Walker, 1999; Walker and Oswald, 2000), is one of many species

projected to suffer range contraction on account of climate change. Models based on the unsophisticated bioclimatic envelope project that *P. strobus*' southern and western range margins will contract in the coming decades (Iverson and Prasad, 1998; Prasad et al., 2007); however, these models could not accurately replicate the current distributions from which they were derived, suggesting that they may be poor predictors of future forest compositions. Furthermore, this prolific species naturally occurs in a wide range of environments (Wilson and McQuilken, 1965; Wendel and Smith, 1990) and thrives outside of the climatic limits within which it is commonly ascribed (Holmes, 1884; Abrams, 2001). The present research is intended to supplant the one-dimensional bioclimatic envelope by identifying spatial variation in *P. strobus*' climatic tolerance. Geospatial analysis of mean sensitivity across the range of a species has the potential to yield such information and further to determine the specific climate variable that precludes complacent growth at a given location.

Dendrochronological records for southern populations of *P. strobus* are scarce; in fact, no *P. strobus* chronology south of Pennsylvania is available in the International Tree-Ring Data Bank (ITRDB). This data gap exists because, in the past, studies of radial growth response to climate neglected the equatorward range limits of species in temperate, humid climates (Chhin et al., 2004). Such limits are usually attributed to competition rather than to climate (Dahl, 1951; Woodward, 1987; Loehle, 1998). Nevertheless, the role of climate in constraining southern range limits and growth rates cannot be ignored (Dahl, 1951; Lesica and McCune, 2004; Hampe and Petit, 2005; Jump et al., 2006). Before geospatial analysis can be performed on *P. strobus* sensitivity, the

dendrochronological record needs to be expanded to include southern sites. Due to the climatically significant elevation gradient across which the species is found in the southern Appalachians (Wendel and Smith, 1990), any study of its southern populations should consider a range of elevation classes. Additionally, the occurrence of disjunct populations in this region (Holmes, 1884; Little, 1971) creates an opportunity to explore *P. strobus*' adaptive capacity. Therefore, the objectives of this study are:

1) to develop chronologies for southern populations of *P. strobus* across an elevation gradient and at a disjunct site;
2) to examine the climatic growth response of *P. strobus* near the southern limits of its distribution;
3) to identify the spatial patterns of mean sensitivity for *P. strobus*; and
4) to define the spatial variability of the species' climatic tolerance.

CHAPTER II

LITERATURE REVIEW

Eastern White Pine

Species Overview

Pinus strobus holds the distinction of having the greatest latitudinal range of any pine species east of the Rocky Mountains (Mirov, 1967). The northern boundary of its distribution runs roughly along the 50th parallel, from Newfoundland, across Quebec and Ontario, and into Manitoba (Figure 2.1) (Mirov, 1967; Wilson and McQuilken, 1965). White pine dominates the forests of New England and New York, where large specimens emerge above the canopy, and where it attains its greatest relative abundance (Spalding, 1899: Abrams, 2001). To the west, the distribution of *P. strobus* surrounds the Great Lakes, reaching its dry margin in southwestern Wisconsin and northeastern Iowa (Transeau, 1905; Ziegler, 1995). From New York and Pennsylvania its distribution juts southward, at ever higher elevations along the Appalachian Mountains, before terminating in northern Georgia and South Carolina (Wendel and Smith, 1990). The prodigious *P. strobus* is a crucial silvicultural component throughout this range (Smith, 1995; Walker, 1999), though it grows most rapidly in the southern Appalachians (Johnson, 1995; Walker and Oswald, 2000).

Historic documents ascribe *P. strobus* to narrow elevational ranges near the southern margin of its distribution. In 1808, it was thought that southern populations of

P. strobus were restricted to an elevational band between 850 and 915 m, while 90 years later *P. strobus* was reportedly found as low as 760 m (Spalding, 1899). Wendel and Smith (1990) attribute the species to elevations as low as 370 m in the southern Appalachians. My observations place the species generally between 650 and 1,070 m near its southern margin. Sporadic and, most likely, planted individuals or clusters are surviving as low as 270 m and as high as 1370 m. Spalding (1899) further reported that white pine in southwestern North Carolina was typically found on south-facing slopes, a finding contradicted by Wilson and McQuilken (1965) who noted that, from Pennsylvania, southward, white pine is usually found on northern aspects. A subject of greater accord is white pine's preference for moist soils and close proximity to perennial water bodies in these southern habitats (Spalding, 1899; Francis, 1979).

The distribution of any species is determined by a dynamic interaction of climatic, topoedaphic, ecological, and historic factors (Hutchinson, 1918; Loehle, 1998; Merriam, 1894). The distribution of white pine is, in part, defined by a mean July temperature between 18 and 23° C (Wendel and Smith, 1990). Annual precipitation within its range is from 51–203 cm, in northern Minnesota and north Georgia, respectively; regardless, precipitation exceeds the rate of evaporation throughout the year (Wendel and Smith, 1990). Soil type does not appear to be limiting, as white pine grows on a wide variety of edaphic conditions; however, it performs best on well-drained, sandy soils (Mader, 1985; Wilson and McQuilken, 1965).

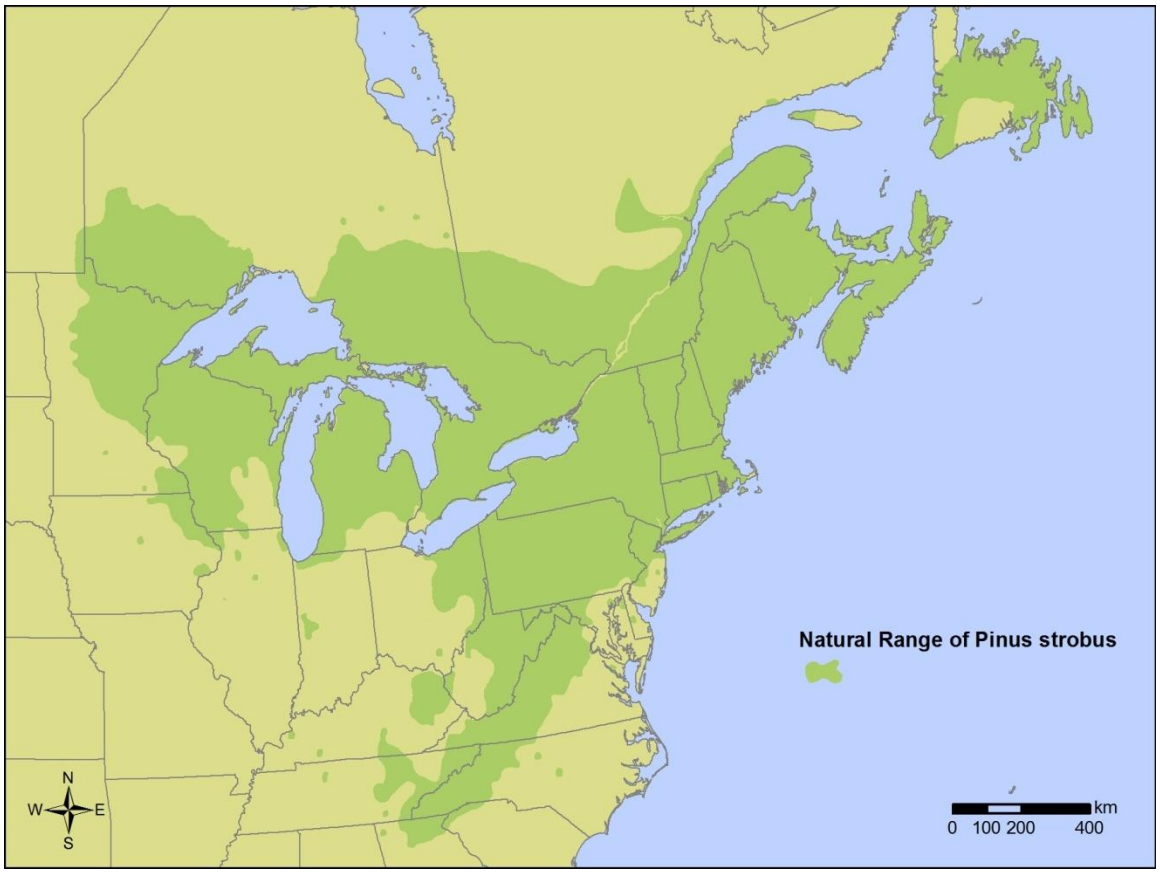

Figure 2.1. Distribution of *P. strobus*.

Ecologically, *P. strobus* has been known to function as a pioneer species, often on abandoned agricultural land or following disturbance (Hilton Green, 1939; Wendel and Smith, 1990; Abrams et al., 1995; Abrams, 2001; Black and Abrams, 2005). Most frequently serving as a successional species, white pine seedlings can rarely compete with their hardwood associates under dense canopies. Nevertheless, many specimens live in excess of 200 years (Wendel and Smith, 1990), thereby reserving a space for themselves in old-growth forests (Smith, 1995). Eschewing its typical role as a successional species, white pine may ascend to the position of climax species on xeric sites with sandy soil (Braun, 1950; Holla and Knowles, 1988; Wendel and Smith, 1990).

Rarely forming pure stands, white pine's common associates in the canopy include *Quercus prinus*, *Tsuga canadensis*, *Acer rubrum*, *Q. rubra*, and *Pinus resinosa* (Wendel, 1980).

Having been described as intermediate in shade-tolerance (Baker, 1949), *P. strobus* initially responds well to increased light (Ballmer and Williston, 1983; Wilson and McQuilken, 1965), but high levels are an impediment, which can blister the thin bark (Walker, 1999). As a result, *P. strobus* is often managed in shelterwood stands to protect specimens from excessive direct sunlight and heat (Walker, 1999). The species also exhibits low tolerance to fire. Evidence shows that white pine was only a minor constituent of pre-settlement forests, even under the clearly favorable climate of the northeastern United States, due to the frequency of Native American and lightning-caused fires (Lutz, 1930; Whitney, 1994; Abrams, 2001). Fire suppression has been credited for its newfound success on sites once thought unsuitable (Abella and Shelburne, 2003; Barrett, 1933).

Despite these constraints, Abrams (2001) believes "that white pine could occupy a range of soil, moisture, and disturbance conditions even wider than those normally associated with this species". Indeed, the species is known to exist in locations with mean July temperatures more than 2° C higher than Wendel and Smith (1990) claim is suitable (cf. Holmes, 1884; Little, 1971). Ziegler (1995) found "vigorous" white pine reproduction, even on southern aspects, at the species' dry, margin. This serves as a reminder, not only of the quantity and complexity of the factors limiting a species'

distribution and ecological function, but of the inadequacy of delineating—whether empirically or statistically—boundaries for such phenomena.

Provenance Studies

Across the range of any widespread species, both ecotypic and clinal variations are evident in its morphology and physiology (Turesson, 1923; Langlet, 1934; Hengeveld, 1990). These variations are usually adaptations to local environmental conditions, increasing the chances of survival or improving reproductive efficacy. Provenance studies have been the preferred method of examining intraspecific variation for over a century (Morgenstern, 1996). Because *P. strobus* was a crucial species in the development of North American silviculture (Pinchot and Graves, 1896), it has been the subject of thorough, decades-long provenance studies (Mergen, 1963; Sluder, 1963; Funk, 1970; Wright, 1970; Garret et al., 1973; Abubaker and Zsuffa, 1990; Genys, 1991; Demerrit and Garrett, 1996). Though none have considered the radial growth of the species, they have, without exception, studied patterns in mortality and in vertical growth.

Growing seedlings—from over 100 locations throughout white pine's range—on plantations in Maryland, Genys (1991) found that those from northern populations suffered the highest mortality rates, with the implication that southern sources were able to cope well with cooler temperatures. In another range-wide provenance study, on a plantation in North Carolina, Sluder (1963) found seedlings from Georgia and North Carolina to have among the lowest mortality rates. Surprisingly, he observed that specimens from nearby Tennessee had a mortality rate nearly four times greater than

those from Georgia. Even those transplanted from as far north as Wisconsin, Michigan, and Maine fared better than the more local Tennessee population. On a plantation in Georgia, average mortality rates were significantly greater than on the higher elevation and higher latitude North Carolina plantation (Sluder, 1963), indicating that heat is limiting across the range of white pine. On the Georgia plantation, as well as on a plantation in Virginia, Nova Scotian and Ontarian specimens had lower mortality rates than even the local specimens, with West Virginia providing the least-fit specimens (Sluder, 1963). The absence of a clear latitudinal trend in these results may be more a reflection of edaphic or hydrologic site factors than of climate.

Genys' (1973) provenance study also examined tree height, which was negatively correlated with latitude of seed source, albeit insignificantly. Nevertheless, the tallest specimens were from Tennessee, North Carolina, and Virginia (Genys, 1983). A network of provenance studies conducted by the U.S. Forest Service confirms that, for a given plantation, southern sources produce the tallest trees (Garrett et al., 1973; Santamour, 1960). Sluder's (1963) study further confirmed these findings, showing a significant, inverse correlation of tree height with latitude of seed source. This trend remains operative for trees grown on plantations to around 43° N; in fact, only one plantation—in Maine—showed a significant, positive correlation of height with source latitude (Garrett et al., 1973). Latitude accounted for as little as 80% and as much as 96% of the variation in height, depending on the plantation. Sluder's study, however, only reported the results for the first three years of growth; therefore, it is noteworthy that this intraspecific variation may represent adaptation to light levels rather than to climate. Under controlled

conditions, Mergen (1963) found the same negative correlation of height growth and latitude, but only when the trees were exposed to light for 16 hours daily. In specimens exposed to an eight hour photoperiod, the same trend was not significant.

Given Mergen's (1963) findings, variation in photosynthetic capacity is one possible explanation for height differences. Indeed, Mergen (1963), Genys (1991), and Garrett et al. (1973) all discovered that specimens from lower latitudes had longer needles. Furthermore, stomate density, that is the number of leaf pores, was higher in southern specimens (Mergen, 1963). Bourdeau (1963) specifically monitored photosynthetic rates and determined that white pines from southern sources photosynthesized more efficiently in low light than those from northern sources; however, cold temperatures caused a reversal of this pattern. Cold also had the effect of reducing the amount of chlorophyll in trees from southern sources, except in those from a disjunct population in central North Carolina, at a site now known as White Pines Preserve. Specimens from White Pines Preserve had chlorophyll concentrations comparable to those of northern specimens (Bourdeau, 1963). All of this supports the assertion that a species' shade tolerance increases equatorward (Baker, 1950; Mayr, 1909). Bourdeau (1963) even claims that *P. strobus* could become shade-tolerant, as opposed to intermediate, in a warm climate.

It would be logical to assume that southern specimens of white pine would be more susceptible than northern specimens to cold-related stress, but the evidence does not always support this. The studies of both Wright (1970) and Garrett et al. (1973) revealed no significant difference among seed sources in their vulnerability to frost or snow

damage. Given the geographically biased nature of such injuries, this finding is quite unexpected. Contrary to these findings, Mergen's (1963) experiments showed southern seedlings experiencing higher incidence of cold damage.

These studies illustrate the high level of climatically-relevant variation found across populations of *P. strobus*. Both clinal and ecotypic expression are evident. While Bourdeau (1963) implied that genetic, and not merely phenotypic factors differentiate *P. strobus* across its range, Mergen (1963) explicitly stated that the disjunct North Carolina population, "by virtue of its specific reaction to many of the experimental conditions to which it was exposed, can probably be classified as a specific ecotype". Nowhere else has such a firm affirmation of ecotypic distinction for this species been published; then again, few studies have examined disjunct populations of white pine. While these provenance studies have ventured to confirm the existence of intraspecific variation, the research designs preclude an understanding of those variations as adaptations to local environmental factors.

Dendroclimatology

Though the aforementioned provenance studies broadly consider growth rates in relation to latitude of seed source, none has quantified white pine's growth response to specific climatic variables. Conversely, dendroclimatologists have explored such relationships, if only for a limited number of stands.

Abrams et al. (2000), studying *P. strobus* on a steep, rocky slope in Massachusetts, discovered that radial growth was significantly correlated with annual

Palmer Drought Severity Index (PDSI), with $r = 0.69$ ($p < 0.05$). They did not consider temperature, but concluded that white pine is sensitive to climate, even near the geographic center of its distribution. Bartholomey et al. (1997) examined *P. strobus* growth response in coastal Maine. Their regression models determined that climate accounted for 25−35% of radial growth; however, when ozone concentrations were included in the model, no climatic variable remained significant. Nevertheless, the climatic variables that seemed to have the strongest effect were summer precipitation, March temperature, and the temperature of the preceding July, all of which exhibited positive relationships with radial growth. Kilgore and Telewski's (2004) research on *P. strobus* in Michigan found no significant response of radial growth to any precipitation variable. In fact, the only significant relationship in their study was with mean April temperature ($r = 0.257$; $p < 0.05$).

Only two studies are known to have investigated climate/growth relationships in *P. strobus* in the southern Appalachians. One of those studies (Vose and Swank, 1994) was of a plantation, ranging in elevation from 700–1000 m. There they found that no climatic variable had a significant impact on radial growth. However, Vose and Swank (1994) also considered soil water potential, which significantly corresponded to growth, with an R^2 value of up to 0.61 ($p < 0.05$), depending on canopy position.

Finally, Hall (2004) evaluated growth of *P. strobus* among eight sites in Georgia, focusing on the impacts of slope and aspect on growth response. The study area was at the southern tip of the species' range and near its lower elevation limit. Nevertheless, comparisons among aspect and slope classes revealed no significant effect from these

presumably relevant factors. Though statistically insignificant, the author did emphasize that growth rates were higher on northern aspects. Also, sites on northern aspects were more highly correlated with one another than were those on southern aspects, indicating greater stress and climatic sensitivity on northern aspects. Correlation analyses of radial growth with climatic variables yielded significant, inverse relationships with summer temperature of the current year and with precipitation in the previous winter. Positive correlations were found with both spring temperature and summer precipitation.

These studies do reveal consistency across the range of *P. strobus*. The authors conclude that high temperatures in the early spring allow *P. strobus* to take advantage of a longer growing season, thereby increasing that year's radial growth (Hall, 2004; Kilgore and Telewski, 2004). Likewise, the importance of summer moisture seems valid throughout the range (Abrams et al., 2000; Bartholomey et al., 1997; Hall, 2004; Vose and Swank, 1994). However, discord persists, such as in Michigan, where Kilgore and Telewski's (2004) study found no precipitation variables to be relevant. No known studies compare climate/growth relationships between populations of *P. strobus*.

Mean Sensitivity

Overview

In order to compare climatic growth response among populations, a single value expressing that relationship would best facilitate statistical analysis. In spite of its previously limited application, the dendrochronological metric of mean sensitivity may

be able to serve in that capacity. Mean sensitivity is simply the amount of interannual variability, or high frequency variation, in ring width for a given core. It is calculated as

$$MS_x = \frac{1}{n-1}\sum_{t=1}^{t=n-1}\left|\frac{2(x_{t+1}-x_t)}{x_{t+1}+x_t}\right|,$$

where *x* is the width of a single ring, *t* is the year of a given ring, and *n* is the number of rings in the series (Fritts, 1976). Verbally, mean sensitivity is calculated as the average "absolute difference between the increments of the current and preceding year divided by the mean of these two increments" (Mäkinen et al., 2001). Values for mean sensitivity, therefore, range theoretically from 0 to 2 and increase with greater variability in ring widths. The mean sensitivity of a site is calculated as the average of the mean sensitivities for all series.

By quantifying this interannual variation, mean sensitivity essentially measures the frequency of years in which environmental conditions constrain growth compared to the frequency of years in which conditions are optimal. That is, if a stand of trees is within a climate that is ideal for growth, mean sensitivity will be low, because interannual fluctuations in weather patterns will not deviate considerably from those ideal conditions. Stands in suboptimal climates, even with similar climatic amplitudes, will yield higher values of mean sensitivity, as conditions in one year may be ideal, but conditions in the next year may preclude cambial division along portions of the bole. Given this pattern, mean sensitivity could be interpreted as a powerful indicator of climatic suitability.

Mean sensitivity was initially proposed by Douglass (1920) as a method of identifying trees that were sufficiently influenced by climate. Sensitive trees were

deemed to be acceptable for use in dendroclimatological evaluations, particularly for climate reconstructions. By convention, mean sensitivity values of greater than 0.3 are representative of sensitive or climatically stressed chronologies (Creber, 1977). Conversely, values less than 0.2 indicate complacent chronologies. One should take note, however, that this delineation between sensitive and complacent values of mean sensitivity is entirely arbitrary; the metric has more objective and intuitive value when compared between or among sites of a given species (Conkey, 1979).

Mean sensitivity continues to be used for the purpose of assessing a chronology's merit in dendroclimatological investigation (Fritts, 1966, 1976; Strackee and Jansma, 1992). However, given the nature of the statistic, and considering the ecological factors that influence it, mean sensitivity has untapped potential as a method of quantifying climatic suitability, or, reciprocally, quantifying how well adapted a population is to its environment.

In their critique of mean sensitivity, Strackee and Jansma (1992) challenged its application in evaluations of macroclimatic tolerance. They alleged that local site factors affect mean sensitivity to an extent that compromises such uses, even though they provided no citation or original data to support this claim. According to Fritts (1976), "Such factors as length of the daylight period, shade, and low amounts of soil minerals, which do not vary significantly from one year to the next, have little influence on the variability in ring width." He further argued that those local factors that affect sensitivity do so by modifying microclimatic conditions. As Fritts (1976) implied, mean sensitivity effectively isolates the role of climate from the suite of environmental factors influencing

radial growth. There remains, however, a need to further examine the hypothesis that local factors supersede the influence of macroclimate on mean sensitivity.

Geographic Patterns

Fritts (1966) developed a graph of dendrochronological statistics—including mean sensitivity—and their relationships with both climate and tree distribution (Figure 2.2). The theories expressed in the graph, however, date to the work of Douglass (1920, 1928, 1936). Fritts (1966) specifically addresses small-scale distributions in semiarid environments as the graph was originally derived from a study in the San Francisco Peaks of Arizona (Fritts et al., 1965). Because of this, he addresses distributions with the terminology "forest interior" and "semiarid forest border." Within the graph, mean sensitivity increases steadily from the forest interior toward the forest border.

One complication in Fritts' (1966) graph is that the trend of increasing sensitivity away from the forest interior suddenly reverses as it crosses the forest border. This is intuitive, since the probability of conditions that prohibit growth in a given year would eventually surpass the probability of favorable growth years in that direction. Beyond a certain climatic threshold, trees—if they could survive at all—would produce consistently narrow rings. However, the arbitrary delineation of the forest border complicates interpretation of the graph.

Another important issue to note is that Fritts (1966) only addresses the semiarid forest border and not the upper elevation, cold border. Using the rationale that sensitivity increases as the probability of favorable conditions in a given year decreases, it is

reasonable to assume that mean sensitivity increases outward in either direction from the interior. Fritts (1966) also neglects trees growing in humid climates or in regions of more subtle topographic relief, where climate varies over greater distances. Nevertheless, no environmental factor would necessarily prevent Fritts' (1966) forest interior and semiarid forest border from acting as proxies for larger scale range cores and range margins, respectively. In fact, dendrochronologists have long asserted that a species' optimal climate is found near the center of its geographic distribution and that mean sensitivity should increase toward range margins (Fritts, 1976; Fritts and Swetnam, 1989; Hart et al., 2010). Unfortunately, few studies empirically examine the geographic patterns of mean sensitivity to test these hypotheses.

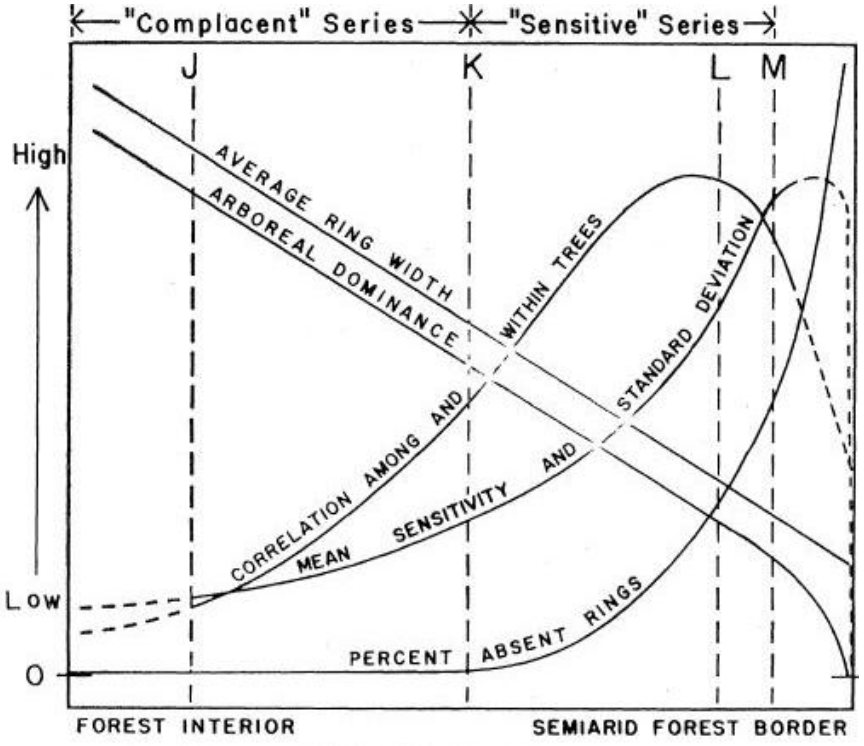

Figure 2.2. Graph of spatial patterns in dendrochronological statistics. (Fritts, 1966)

Although most studies that report values for mean sensitivity present no analysis of the statistic, data from such papers can be synthesized to derive an understanding of geographic patterns of mean sensitivity. Providing empirical support for his idealized graph, Fritts (1976) compiled data from *Pinus longaeva* chronologies in the White Mountains of California. At these sites, elevation was the dominant environmental gradient. On a northern aspect, mean sensitivity increased toward both elevational extremes (Fritts, 1969). Also studying *Pinus longaeva* across an elevation gradient, LaMarche (1974) confirmed that mean sensitivity is lowest in the forest interior and increases toward both the upper- and lower-elevation treelines. Peng et al. (2008), working with *Sabina przewalskii* on the Tibetan Plateau, reported a trend of declining sensitivity from low- to high-elevation forest boundaries, although with a slight increase at the upper-elevation treeline. Wang et al. (2005), in their study on *Picea schrenkiana* in the Tianshan Mountains of China, found that mean sensitivity decreased consistently with increasing elevation. Each of these small-scale studies only considered sites within semiarid climates. Larger scale studies and those examining species in temperate, humid environments are rarer.

At a slightly broader geographic scale, Zhang and Hebda (2004) examined radial growth of *Pseudotsuga menziesii* near the central coast of British Columbia. In this wet environment, where temperature is the dominant climatic component affected by elevation, a clear pattern emerges for mean sensitivity. The lowest elevation sites yield the highest values for mean sensitivity, with similar values for the upper-elevation treeline. At the central elevations, mean sensitivity is at its lowest. Of the nine sites

studied, a single mid-elevation site with a uniquely high mean sensitivity is the sole exception to this trend.

In the similarly cool and wet environments of the Pacific northwestern United States, Peterson et al. (2002) found no elevational pattern of mean sensitivity for chronologies of *Abies lasiocarpa*. However, the authors did not report values of mean sensitivity in their paper, nor did they discuss the method by which they determined that no pattern existed. The expected non-linear trend of mean sensitivity across an elevation gradient would not be identified by simple correlation or linear regression, which are the quantitative methods used by Peterson et al. (2002) to explore climatic relationships with ring width.

Di Filippo et al. (2007) examined chronologies of *Fagus sylvatica* over a large region of the eastern Alps. This was not a range-wide study, though, as the species is found as far away as northern Spain, Sicily, Scandinavia, and the Black Sea. The study did, nevertheless, capture the elevational range of the species. The authors found that mean sensitivity increased from mid elevations toward both upper- and lower-elevation extremes. The highest values of mean sensitivity occurred at the upper-elevation limits.

Falcon-Lang (2005) looked at global patterns of mean sensitivity for 554 tree-ring chronologies selected randomly from the ITRDB. These chronologies represent 83 species of conifer. He expressed difficulty in quantifying patterns, because of mean sensitivity's complicated relationship with climate. Even so, he noted that the highest mean sensitivity values were found in cold, dry climates, even though these environments

exhibited a wide range of sensitivity values, from 0.15 to 0.75. Conversely, the lowest values for mean sensitivity were found in warm, wet climates.

Falcon-Lang (2005) identified four global regions in which values of mean sensitivity tend to be at their highest. The first of these regions is mid-elevation sites in the southwestern U.S., especially those where *Pseudotsuga menziesii* dominates. The northern regions of Russia, where species of the genus *Larix* are abundant, constitute the second region. The higher elevations of northern Britain and the Alps also exhibit high mean sensitivities. Finally, the warm, wet climate of the southeastern United States produces a considerable number of sensitive conifer chronologies, which contradicts the long-held assumption that wet, temperate climates will consistently stimulate complacent growth (see: Fritts, 1976). The author's additional finding that high and low values of mean sensitivity were often located in close proximity to one another is most likely because he included dozens of species in a single analysis. One should not expect to discover obvious geographic trends in values of mean sensitivity across species, just as one would not expect geographic distributions or radial growth response to be identical across species (cf. Gleason, 1926; Graumlich, 1993; DJalilvand, 1996; Friend and Hafley, 1998).

Hart et al. (2010) specifically addressed the geography of mean sensitivity in *Tsuga canadensis* chronologies. *T. canadensis* has a geographic distribution that is nearly identical to *P. strobus*, and their climatic constraints are similar (Burns and Honkala, 1990). Working under the assumption that sensitivity should increase toward the margins of a species' distribution and in disjunct populations, the authors analyzed

the metric across all chronologies available in the ITRDB. Conspicuously missing from this and from every other known assessment of dendrochronological patterns, however, is rigorous geospatial analysis. The authors' only statistical assessment consisted of *t*-tests to determine whether the chronology from a disjunct population revealed a significantly different mean sensitivity from that of its nearest neighboring chronology or from the average mean sensitivity for all sites. They found no such difference and concluded that microclimatic conditions were similar between the disjunct site and the range core. However, an alternative inference is that genetic isolation has allowed the disjunct population to evolve a unique climatic response. Perhaps the population falls to the far right of Fritts' graph, where sensitivity decreases once outside the theoretical "forest border". Differences in soil structure or chemistry could account for the findings. Regardless of alternatives, the authors' conclusion does not follow inevitably from the results. More detailed geospatial analysis could have elucidated an underlying pattern of mean sensitivity.

As seen here, peripheral specimens tend to be more sensitive to climate than specimens found at the center of a species' range, according to their relative values of mean sensitivity. However, one should be careful not to conflate geographic and environmental margins, as site factors and genotypic variation may be able to modify this relationship (see: Colie, 1936; Fritts, 1976; Villalba et al., 1994; Henderson and Grissino-Mayer, 2009; Hart et al., 2010). Nevertheless, the literature seems to support Fritts' (1966) graph and even its broader application to upper elevation limits and to species in

wet climates. Given the geographic constraints of existing dendrochronological work, however, there is still a need to explore range-wide patterns of mean sensitivity.

CHAPTER III

METHODS

Southern Chronologies

Study Area

Pinus strobus chronologies were developed for four sites in North Carolina. Three sites are located on the western slope of Linville Mountain, in McDowell County, North Carolina, within Pisgah National Forest (Figure 3.1). The mountain rises from an elevation of roughly 400 m to peaks of over 1200 m, encompassing the entire elevation range of *P. strobus*. The 800 m gradient on a single mountain provides the ideal opportunity to examine the species at different elevations while minimizing the variation of extraneous factors. Therefore, at this location, *P. strobus* was studied within three elevation classes: 400–450 m, 775–825 m, and 1150–1200 m.

Slopes on the mountain are on average 10–30°, but can be much higher. Aspect is generally western, though both northern and southern aspects are common. At Linville Mountain, *P. strobus* associates most frequently with *Quercus prinus* (LANDFIRE, 2010). Other common tree species in the area include *Tsuga canadensis*, *Liriodendron tulipifera*, *Q. rubra*, *Q. alba*, and *Q. velutina* (LANDFIRE, 2010). Soils are mostly of the Ditney, Soco, and Unicoi series (Web Soil Survey). Weathered from quartzite and phyllite, these well-drained inceptisols contain 15–65% rock fragments and are moderately suited to woodland growth (Mathis, 1995).

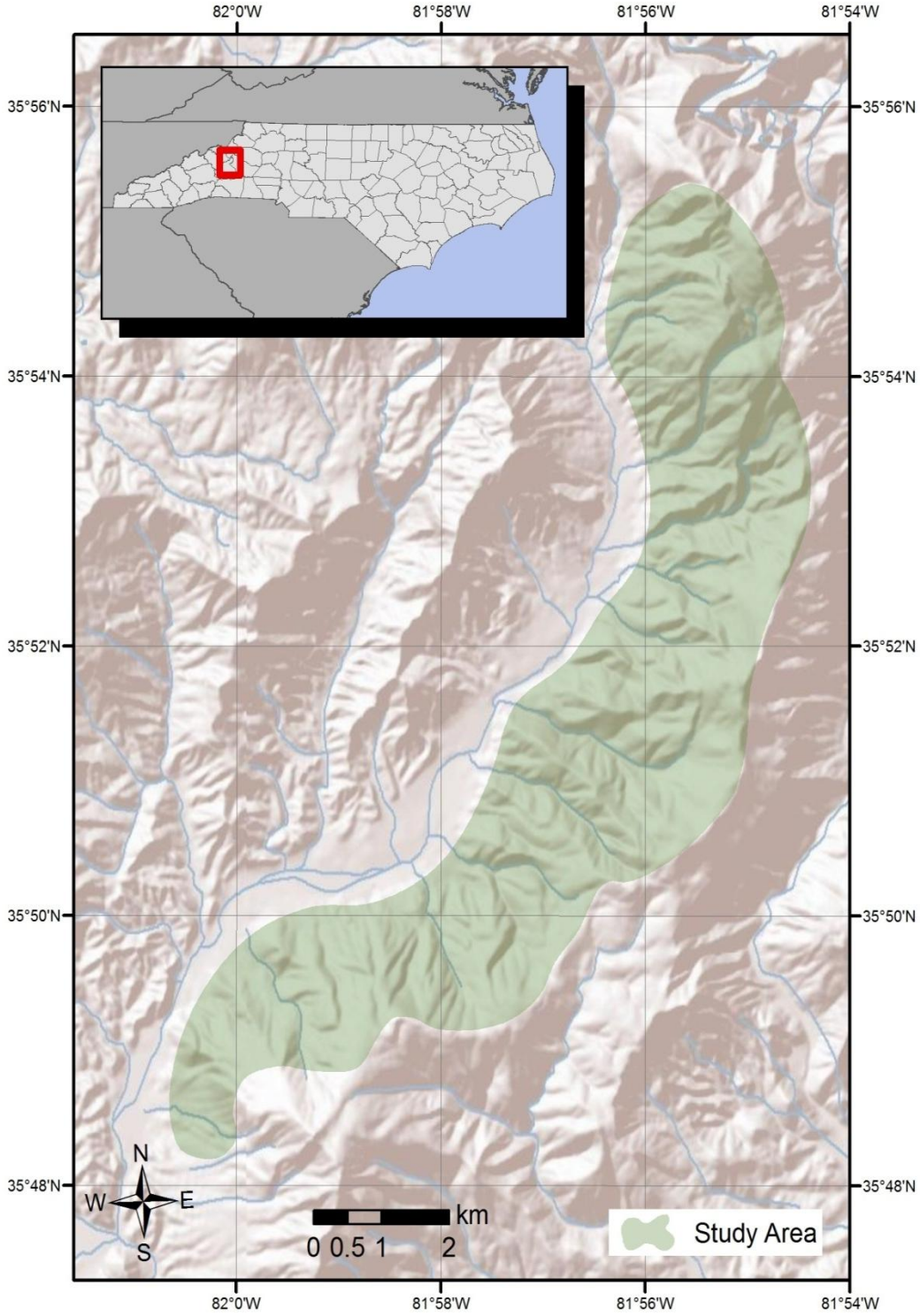

Figure 3.1. Linville Mountain study area.

At an elevation of roughly 800 m, the nearest weather station, in Celo, NC, should provide a fairly accurate representation of conditions on Linville Mountain, even though differences in orographic conditions could have some mitigating effect. Data from this station indicate an annual mean temperature of 11.0° C, a July mean temperature of 20.8° C, and a mean January temperature of 1.0° C (Southeast Regional Climate Center). The temporally well-distributed precipitation averages 148 cm yr^{-1} (Southeast Regional Climate Center).

The fourth site (Figure 3.2), operated by the Triangle Land Conservancy and known as White Pines Preserve, lies at the confluence of the Deep and Rocky Rivers, in Chatham County. At elevations of 60–120 m, the steep, north-facing slopes here host an assortment of mountain disjunct tree and shrub species, including *P. strobus*, isolated since the Pleistocene (Beard, 1959; Hardin and Cooper, 1967; Swab, 1990). The *P. strobus* population here has been recognized for its uniqueness since Holmes (1884) first reported on it in a single paragraph blurb. Since then, it has received minor treatment in provenance studies (Bourdeau, 1963; Mergen, 1963) but little other examination.

Most of the *P. strobus* at this site grow on north-facing slopes. Although they can be found in uplands, where they associate with *Fagus grandifolia*, *Quercus rubra*, and *Q. alba*, *P. strobus* are most prominent on the steep bluff bordering the Rocky River, where they tower over an open canopy of *Q. montana*, *Q. rubra*, and *Q. coccinea* (Swab, 1990). The predominant soils at this site are of the Badin and Nanford series, with slopes ranging from 6–30% (Web Soil Survey). These well-drained, upland ultisols were developed from fine-grained meta-volcanic bedrock. They are well suited to woodland

growth; however, the shallow Badin soil limits root penetration, making the trees susceptible to windthrow (Hayes, 2006).

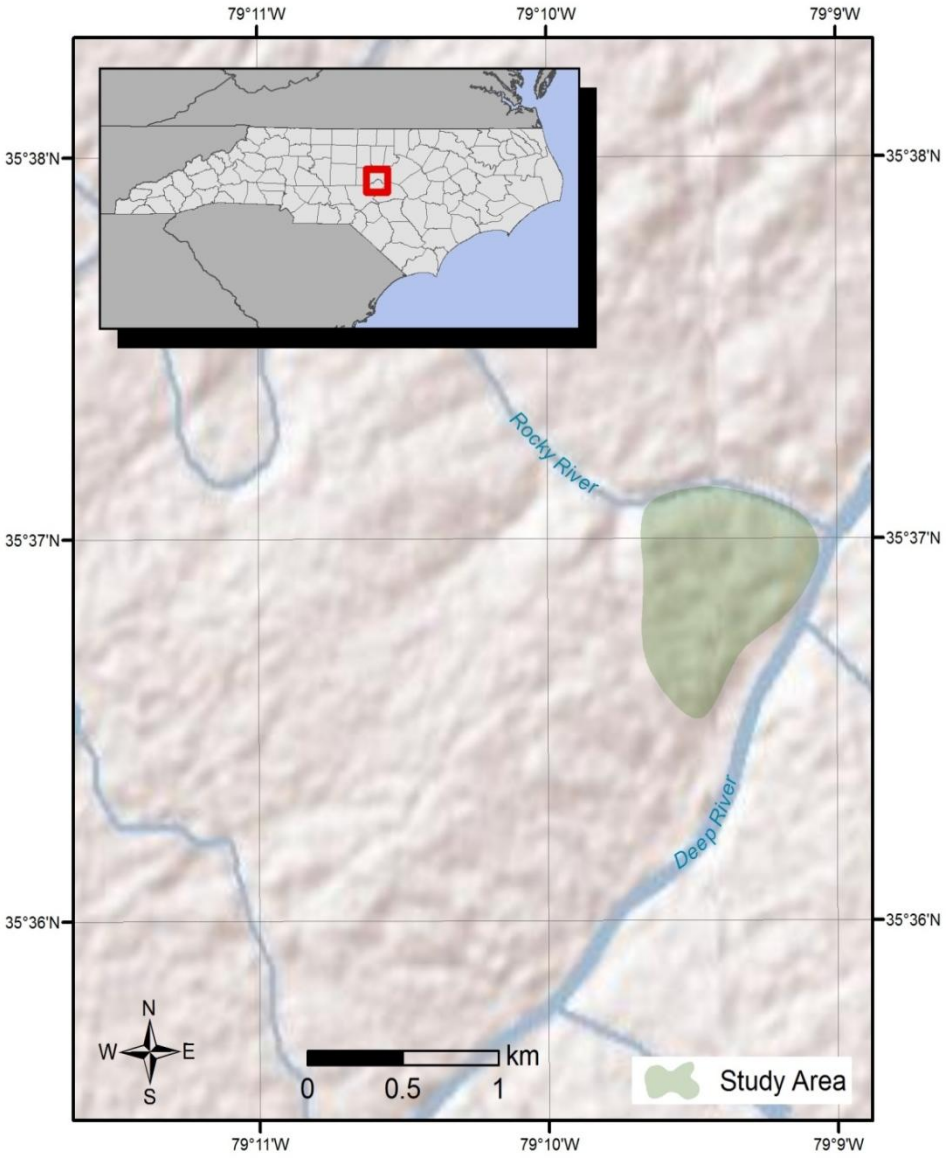

Figure 3.2. White Pines Preserve study area.

Climate data from the nearest weather station, in nearby Sanford, NC, have a mean annual temperature of 15.6° C, with a mean July temperature of 26.0° C, and a

mean January temperature of 4.9° C (Southeast Regional Climate Center, 2010), although researchers have posited that microclimatic conditions at White Pines Preserve maintain substantially lower temperatures than the surrounding area (Swab, 1990; Hardin and Cooper, 1967). Precipitation, which averages 118 cm annually, is evenly distributed throughout the year, with a slight peak in the summer months (Southeast Regional Climate Center, 2010).

Field Methods

Dendrochronological field methods adhered to the standards outlined by Phipps (1985) and Stokes and Smiley (1996). All cores were collected during the summer and autumn of 2010. Two cores per tree were extracted from fifteen specimens at White Pines Preserve and at each elevation class on Linville Mountain for a total of 60 trees and 120 cores. Dominant specimens were selected, to maximize the climatic signal (Cook and Kairiukstis, 1990). Trees showing evidence of any abnormal growth patterns, infections, or major scarring were avoided. For a given tree, the two cores were taken at a 180° angle from one another and parallel to the contour. GPS coordinates, diameter at breast height, slope, and aspect were documented for each tree.

Lab Methods

Cores were air dried, mounted with the transverse plane visible, and progressively sanded to reveal their cellular structure. Samples were crossdated using the list method (Yamaguchi, 1991); COFECHA was later employed to verify cross-dating accuracy

(Holmes, 1983). Ring widths were measured to the nearest 0.001 mm. The raw measurements were standardized in ARSTAN (Cook, 1985), using a conservative negative exponential curve (Cook and Holmes, 1986) in order to reduce the signal of age-related growth trends; however, each series was examined individually to verify the suitability of the negative exponential curve. In situations where suppression and/or release were evident in the graph of radial increments, the negative exponential curve was deemed inappropriate. In such cases, alternate detrending methods, such as a Hugershoff growth curve (Warren, 1980) or Friedman variable span smoother with a conservative alpha (Friedman, 1984) were used. Standard mean chronologies were then derived for each site and elevation class, using the biweight robust mean (Cook, 1985; Cook and Kairiukstis, 1990).

Climate Data

Climate division data for each site were acquired from the National Climatic Data Center (NCDC; 2010). The Linville Mountain sites all fall within North Carolina Division 1, while White Pines Preserve is within North Carolina Division 4. Climatic variables included mean monthly temperatures, monthly precipitation, and monthly Palmer Drought Severity Index (PDSI) values. Monthly climate variables for a twenty-one month window, from the previous March through November of the current year, were considered for each year in the chronologies, since conditions in the preceding year can influence growth via preconditioning (Fritts, 1976).

Data Analysis

Dendroclimatic analyses were performed in DENDROCLIM2002 (Biondi and Waikul, 2004). Correlation functions and response functions were calculated for the chronologies and the climatic data. Correlation functions are simply sequences of Pearson's correlation coefficients between the chronology and monthly climate variables. A response function, on the other hand, is essentially a principal components regression, which removes the effects of multicollinearity in the independent variables (Fritts, 1976; Briffa and Cook, 1990). DENDROCLIM2002 uses bootstrapped confidence intervals for the correlation and response functions, accounting for serial autocorrelation in the chronologies, and rectifying some of the problems with traditional methods of assessing statistical significance (see: Cropper, 1985; Guiot, 1991).

Given the objections to correlation and response functions (Biondi, 1997; Blasing et al., 1984), climatic growth responses were also analyzed using moving correlation and moving response functions, as outlined by Biondi (1997; Biondi and Waikul, 2004). This helped to identify any potential temporal variability in climatic responses. Such moving interval analysis "employs a fixed number of years progressively slid across time to compute the…coefficients" (Biondi, 1997). Otherwise, it is identical to standard correlation and response function analyses. A window length of 42 years was selected for moving interval analysis, because this was the minimum interval permitted by the software, given the number of independent variables under examination.

Mean Sensitivity

Local Factors

In order to determine the influence of local factors on mean sensitivity, I examined the individual tree data from the four North Carolina chronologies of *P. strobus*. Since slope and aspect are the most readily quantifiable, non-climatic features that Fritts (1976) argues can influence mean sensitivity, they were the measures explored here. For each pair of cores acquired from a given tree, I calculated the average mean sensitivity. The slope and aspect of each tree had been measured and documented *in situ*. Aspect was transformed to a linear measure of southern exposure, by the formula

$$x = |180 - y|,$$

where y is the azimuth of the aspect. Such a transformation yields low values for southern aspects and higher values for more northern aspects, with a range of 0−180. By addressing the inherent problems of analyzing angular data (Cain, 1989), this transformed aspect serves as a simple and efficient, albeit imperfect, proxy for both potential insolation and moisture availability. In this conversion, east and west are considered to be equal, which is an acceptable sacrifice given the nature of the analysis and regional weather patterns (cf. Ike and Huppuch, 1968).

In order to examine the influence of topography at multiple scales, 30 m raster data for elevation, slope, and aspect were acquired from LANDFIRE (2010). In ArcGIS, each tree was attributed with the elevation, slope, and aspect values of the cells over which it lied. The aspect values were then transformed, as above, to linear measures of

southern exposure. For each of the four study sites, Pearson's correlation coefficients were then calculated between mean sensitivity and each of the five site metrics: slope and southern exposure as measured *in situ*, along with elevation, slope, and southern exposure as interpolated by LANDFIRE (2010). The individual tree data were then aggregated among the four sites, and Pearson's correlations coefficients were calculated for this more comprehensive dataset as well.

Dendrochronological Data

To explore the broad-scale geographic patterns of mean sensitivity in humid, temperate environments, data on 33 *P. strobus* chronologies, including geographic coordinates and elevation, were downloaded from the International Tree-Ring Data Bank (ITRDB). The four North Carolina chronologies were included, for a total of 37 chronologies from throughout the species' range.

The distance of each chronology site to the species' range margin was calculated in ArcGIS, using a near analysis. The data used to determine the geographic distribution was Little's (1971; USGS, 1999) range map; however, the range shapefile had been modified so that lakes and rivers falling entirely within the climatic realm of *P. strobus* would not constitute range boundaries.

Climate Data

Gridded data for climate normals from 1971–2000 were downloaded from the PRISM Climate Group (2004) and converted to 800 m-resolution raster datasets. These

data were of annual precipitation, mean maximum temperature, and mean minimum temperature. The precipitation data were converted to centimeters. A mean annual temperature raster was calculated from the maximum and minimum temperature datasets. The resulting temperature raster was then converted to express degrees Celsius, rounded to the nearest hundredth. Since these climate data were only relevant to chronologies within the United States, data that would cover Canadian chronologies were downloaded from the Soil Landscapes of Canada Working Group (SLC; 2007). Climate normals for 1961–1990 were joined to the ecodistrict-level SLC data. Despite the different time-frames of the available data for the U.S. and Canada, a ten year discrepancy should not significantly compromise the results. The Canadian data were also converted to express precipitation in centimeters and temperature in degrees Celsius. Using ESRI's ArcGIS, the chronologies were attributed with the appropriate climate data.

Data Analysis

For the set of 37 *P. strobus* chronologies, Pearson's correlation coefficients were then calculated between site-level mean sensitivity and six geographic attributes: 1) latitude, 2) longitude, 3) elevation, 4) average annual precipitation, 5) mean annual temperature, and 6) distance to the range margin. This process would identify variables that have a linear, range-wide impact on ring-width variability.

A global, ordinary least-squares (OLS) regression was run from ArcToolbox, with mean sensitivity as the dependent variable. The ultimate goal was to examine the geographic heterogeneity of climatic response via geographically weighted regression

(GWR), rather than to most accurately predict values of mean sensitivity. Thus, only average annual precipitation and mean annual temperature were used as independent variables. Latitude, longitude, and distance to range margin would have been redundant in a GWR and would have thwarted attempts to interpret the output. The global regression residuals were assessed via calculation of Moran's *I* (Anselin, 1995) to determine whether spatial autocorrelation was present in the prediction error (Zhang et al., 2005; Osborne et al., 2007; Windle et al., 2009). Clustering of the residuals would indicate spatial non-stationarity, or regional differences in the influence of independent variables (Fotheringham et al., 2002; Jetz et al., 2005; Zhang et al., 2005).

Since spatial non-stationarity was suggested by the results, GWR (Fotheringham et al., 2002) was employed using the same variables. In previous studies, GWR improved the global regression predictions and accounted for spatial non-stationarity (Zhang et al., 2004; Zhang et al., 2005; Osborne et al., 2007; Wimberly et al., 2008). I performed GWR within ArcGIS 9.3, using an adaptive kernel bandwidth that minimized the corrected Akaike Information Criterion (AICc; Hurvich et al., 1998) and then again with a fixed kernel bandwidth that minimized the AICc. The residuals were assessed via Moran's *I* to determine in which model their spatial autocorrelation was lowest (Zhang et al., 2005), i.e., which model best accounted for spatial heterogeneity of climatic tolerance.

For the best-fit GWR, rasters were generated of the resulting coefficients and of the intercept. Also, predictions were made across a grid of points, at a spacing of 10 km, throughout the range of *P. strobus* in order to estimate the mean sensitivity throughout

the species' range. These predictions were based on the GWR model and local values of annual precipitation and mean annual temperature. The output data for coefficients and predictions were examined visually to interpret the spatial patterns of *P. strobus* sensitivity as it relates to precipitation and temperature.

CHAPTER IV

RESULTS

Southern Chronologies

Linville Mountain, Low-Elevation Site

Of the 30 cores acquired at the low-elevation Linville Mountain site, only 23 could be measured and cross-dated adequately. The remaining cores were unusable because of excessive resin or fractures, or because they correlated poorly with the site chronology. The chronology ranged 141 years, from 1869–2009 (Table 4.1). The mean series length was 54.7 years. Inter-series correlation was 0.573, and the average mean sensitivity was intermediate (see: Creber, 1977) at 0.262, both of which indicate that the chronology is moderately suited to dendroclimatological investigation (Fritts, 1976; Grissino-Mayer, 2001). Low-sample depth prevented further consideration of rings formed prior to the year 1930.

Correlation analysis revealed this site to be most sensitive to spring temperature (Figure 4.1). Specifically, growth responds positively to March temperature ($r = 0.37$; $p < 0.05$). Interestingly, March temperature of the previous year has the opposite effect ($r = -0.26$; $p < 0.05$). Previous June temperature is positively correlated with growth as well, but neither of these antecedent conditions was found to be significant in the response function analysis (Figure 4.2). Current March temperature remains significant, even under the more discriminating response function analysis. Precipitation is

significantly correlated to growth only for the month of July ($r = 0.28$; $p < 0.05$; Figure 4.3). This relationship remains significant in the response function analysis (Figure 4.4), but at a reduced strength ($r = 0.22$; $p < 0.05$). No monthly PDSI value significantly affected growth rates (Figs. 4.5 and 4.6).

Moving correlation functions revealed that the relationship of growth with March temperature—in both the previous and current years—is temporally consistent (Figure 4.7). The moving response function showed that the negative response to previous March temperature was only significant for a brief period of time, during which the positive response to current March temperature became less important (Figure 4.8). The only notable precipitation variable in the moving interval analysis was that of the previous September (Figs. 4.9 and 4.10). In the early part of chronology, September precipitation had a positive effect on growth, but this effect has not been evident in recent decades. PDSI has not had any sustained effect on growth at this site (Figs. 4.11 and 4.12).

Site	Start Year	Interseries Correlation	Mean Sensitivity	Serial Autocorrelation
Low Elevation	1869	0.573	0.262	0.651
Mid Elevation	1884	0.488	0.213	0.712
High Elevation	1919	0.466	0.205	0.736
White Pines Preserve	1848	0.611	0.218	0.719

Table 4.1. Chronology statistics for all four study sites.

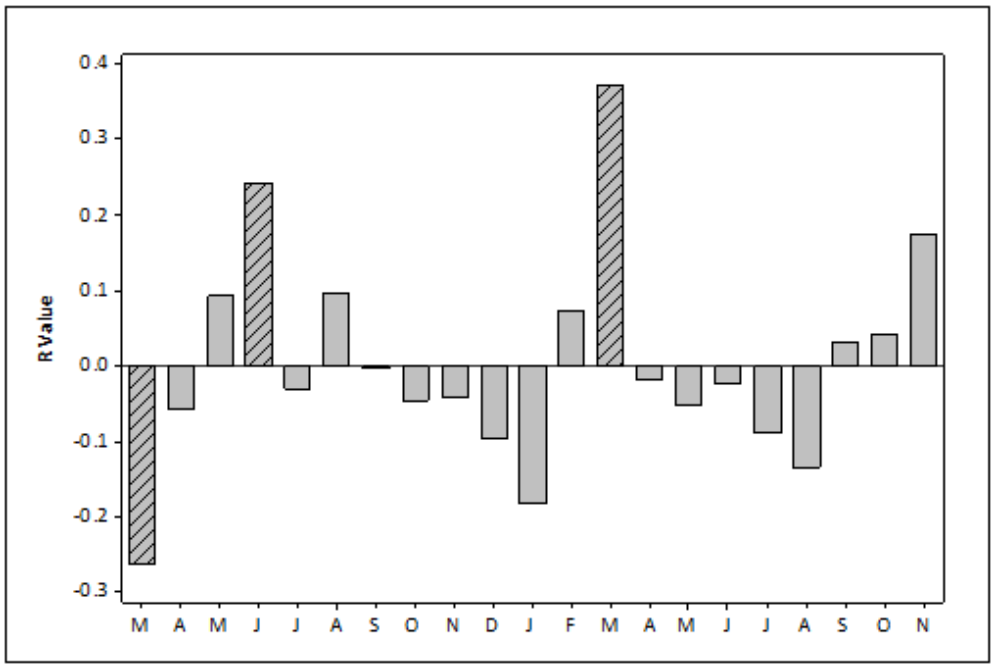

Figure 4.1. Correlation of temperature and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

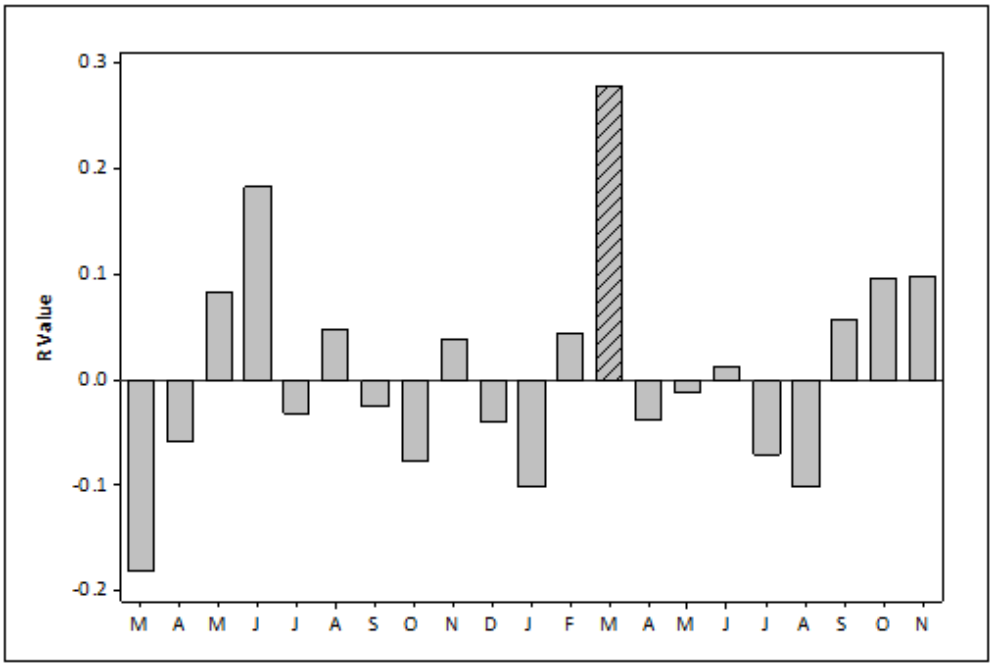

Figure 4.2. Response function of temperature and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

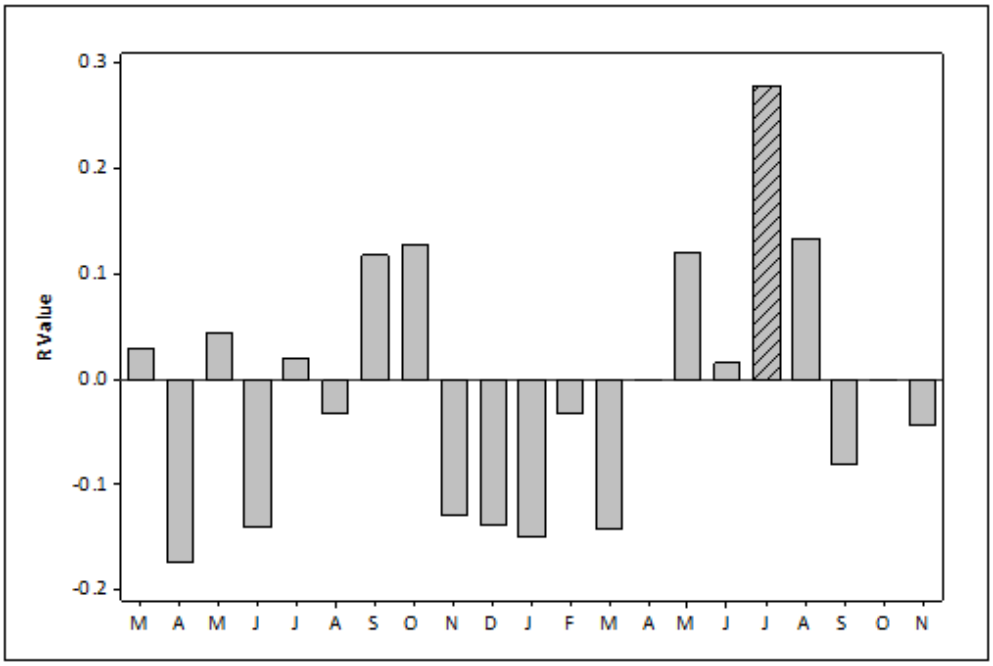

Figure 4.3. Correlation of precipitation and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

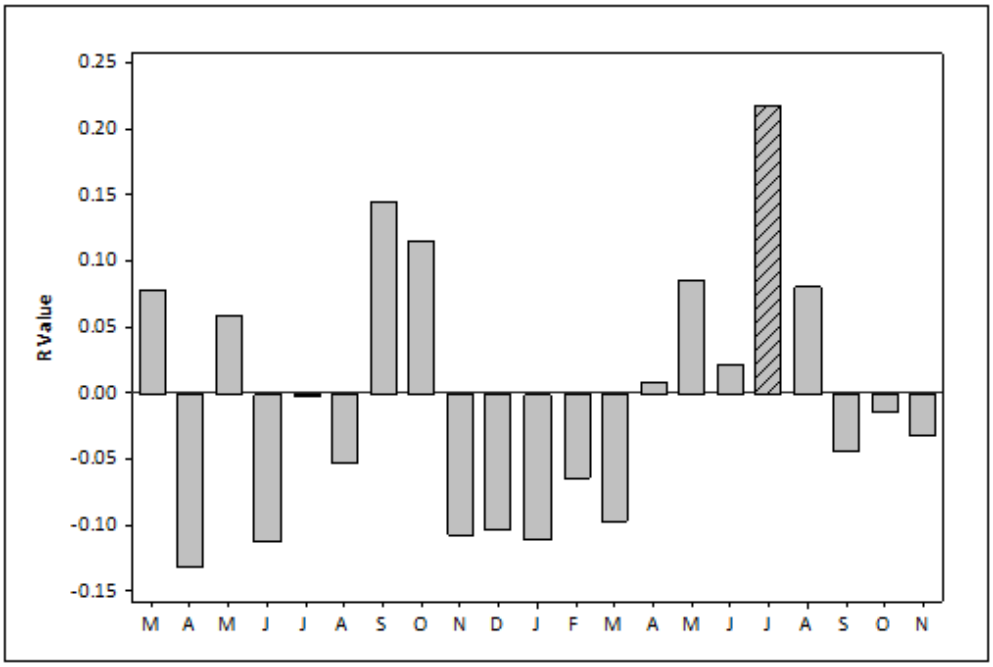

Figure 4.4. Response function of precipitation and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

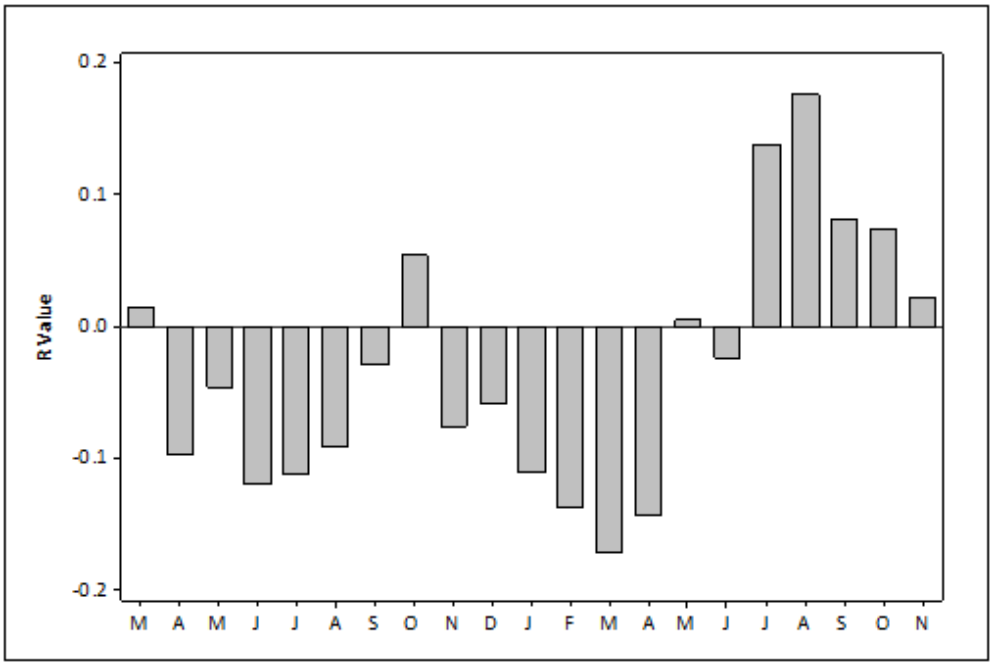

Figure 4.5. Correlation of PDSI and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

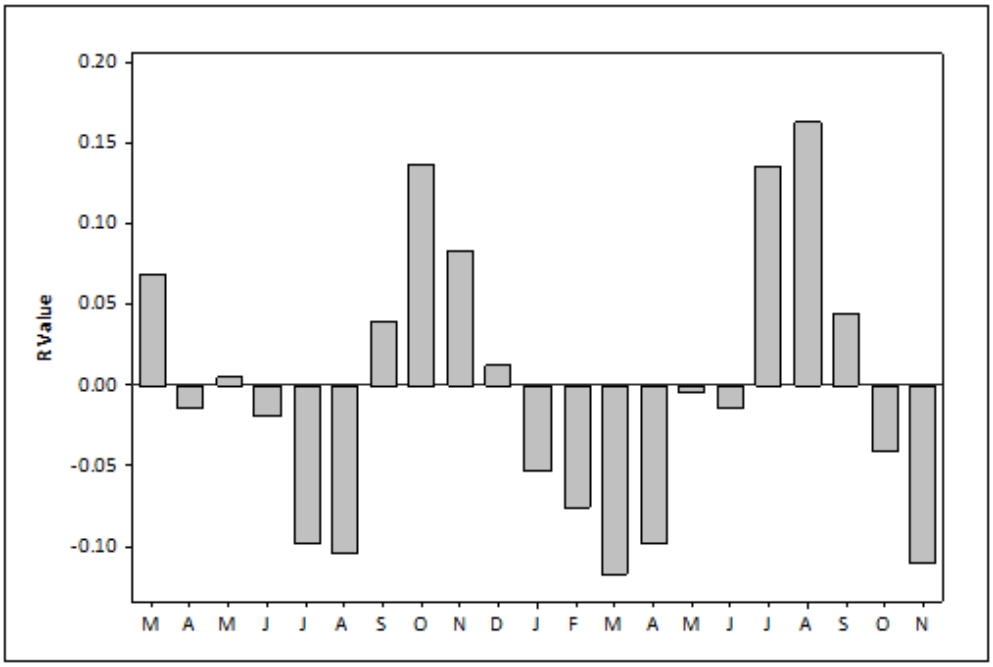

Figure 4.6. Response function of PDSI and growth at low-elevation site. Hachured bars represent significance, at $p < 0.05$.

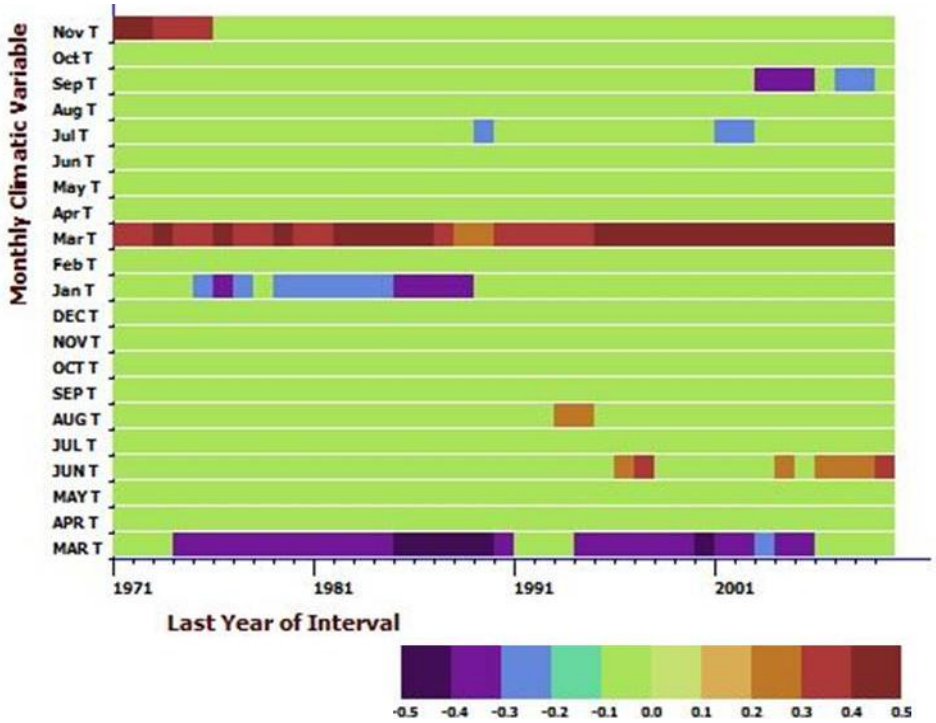

Figure 4.7. Moving correlation of temperature and growth at low-elevation site.

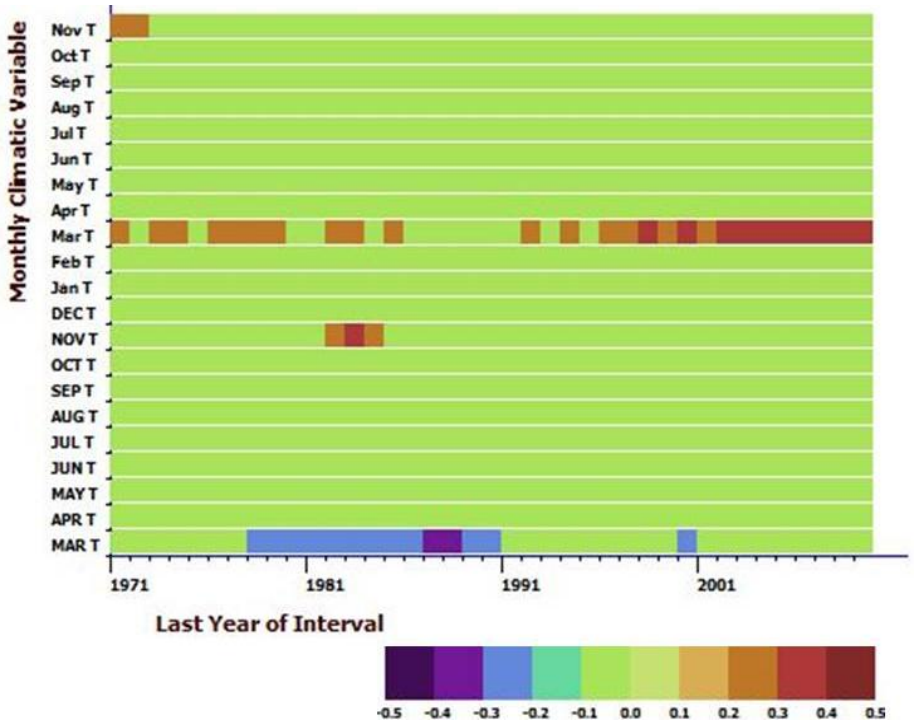

Figure 4.8. Moving response function of temperature and growth at low-elevation site.

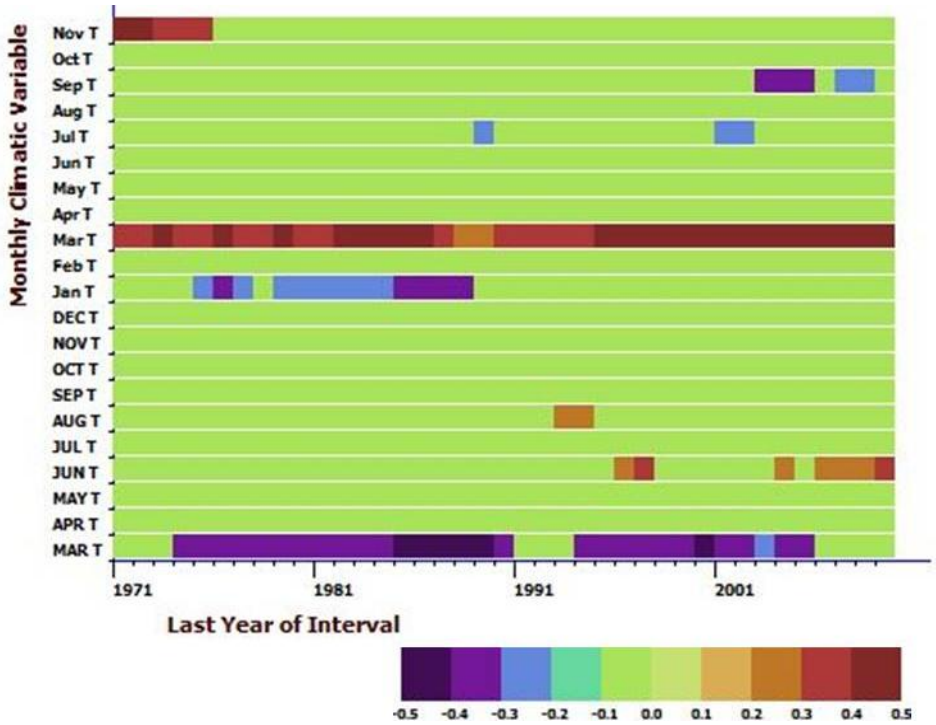

Figure 4.9. Moving correlation of precipitation and growth at low-elevation site.

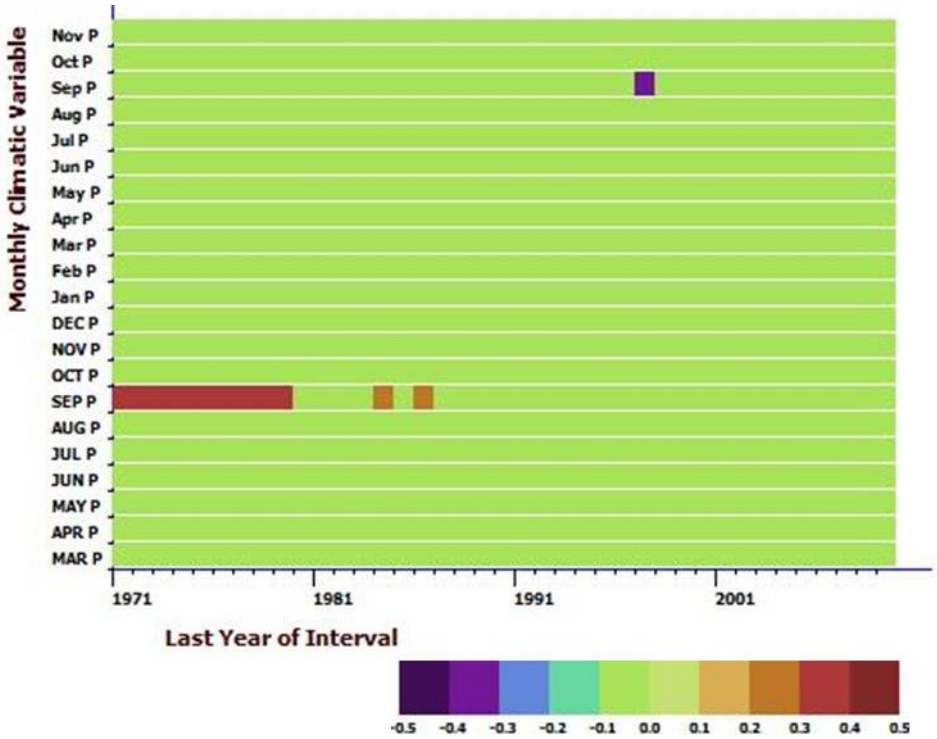

Figure 4.10. Moving response function of precipitation and growth at low-elevation site.

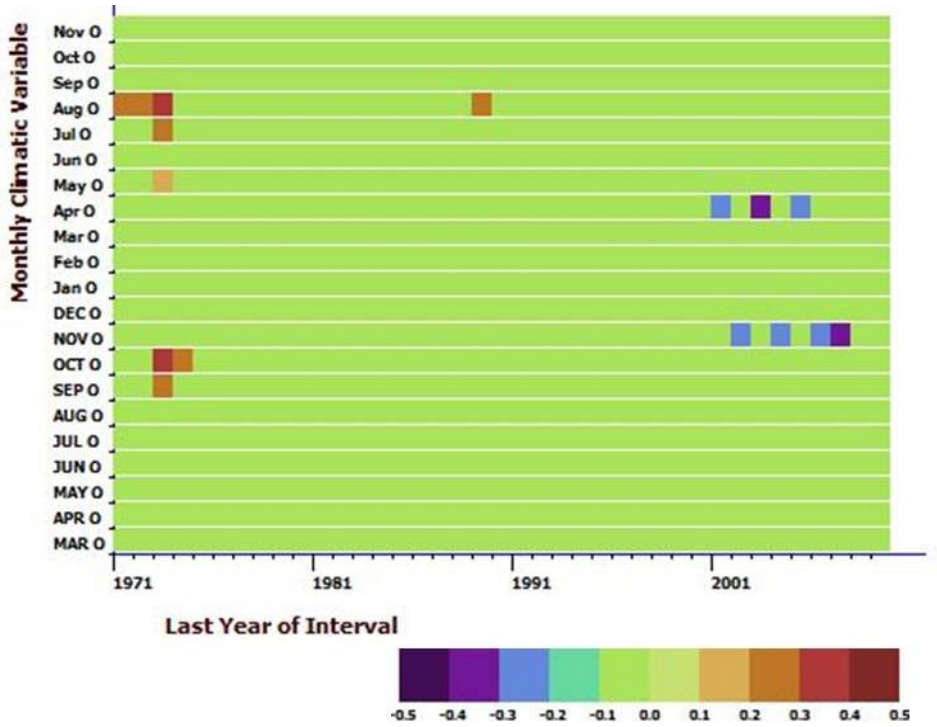

Figure 4.11. Moving correlation of PDSI and growth at low-elevation site.

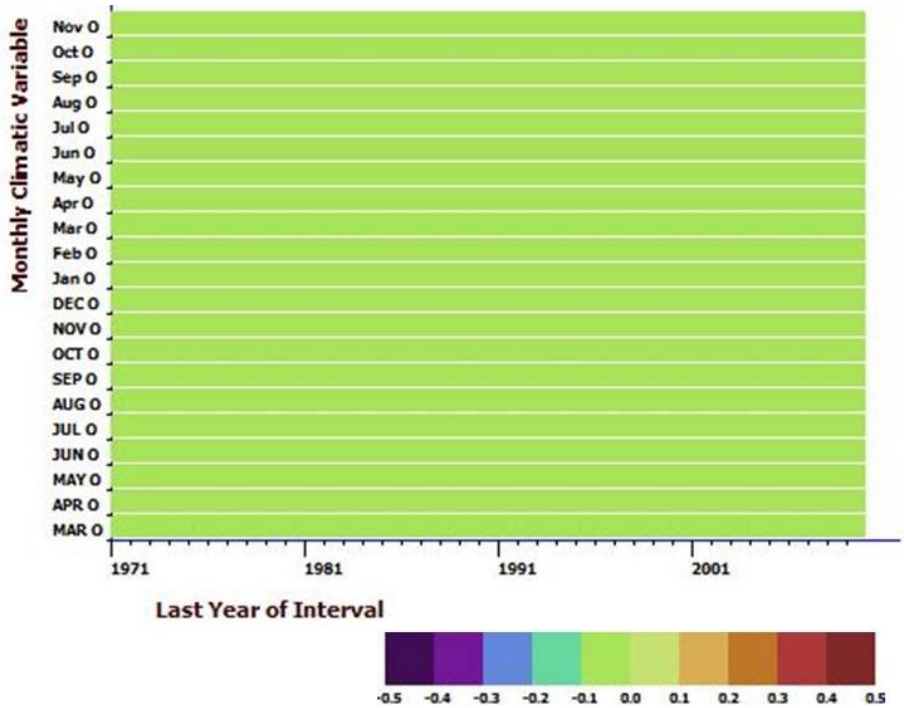

Figure 4.12. Moving response function of PDSI and growth at low-elevation site.

Linville Mountain, Mid-Elevation Site

The mid-elevation site at Linville Mountain yielded a chronology comprised of 29 series (Table 4.1), extending from 1884–2009, with a mean series length of 72.3 years. The inter-series correlation and mean sensitivity were both comparatively low, at 0.488 and 0.213, respectively. This suggests that radial growth at this site is less affected by climate than at the low-elevation site. Given Fritts' (1976) figures, this chronology would be of questionable merit in climate reconstruction. Due to low sample depth prior to 1937, that period was omitted in analyses.

As in the low-elevation site, temperature seems to have a stronger effect on growth than moisture (Figs. 4.13–4.16). Specifically, March and April temperature are positively correlated with growth, at $r = 0.29$ ($p < 0.05$) and $r = 0.24$ ($p < 0.05$),

respectively. Precipitation of the previous June is negatively correlated with growth (r = 0.23; $p < 0.05$). No monthly value of PDSI is significantly correlated with radial increment (Figs. 4.17 and 4.18). The response function analysis revealed only a single monthly climate variable—March temperature—to influence growth.

Moving correlation analysis revealed the decreasing importance of April temperature and the increasing importance of temperature during October and the previous September (Figure 4.19). While April and October temperature both had a positive effect on growth, warmer temperatures in the previous September seem to inhibit radial growth. During the 42 year period ending in 2009, growth was only correlated to temperature in October. Moving response functions reinforced the shift in importance from April to previous September (Figure 4.20).

No trend is evident in the moving correlation or response functions of precipitation, except that previous July precipitation has become weakly, positively correlated with growth during the last 50 years (Figs. 4.21 and 4.22). Precipitation during both May and July of the current year were strongly, but only briefly correlated with growth. PDSI of the previous May and June were shown to be negatively correlated with growth in the early part of the chronology (Figure 4.23). In recent years, high values of PDSI in the early growing season reduce annual growth. The counterintuitive, negative correlations with PDSI present a challenge to understanding the growth dynamics at this site. Moving response functions, however, did not indicate any notable negative effect of PDSI (Figure 4.24). Instead, they revealed a brief period when August PDSI was positively correlated with growth.

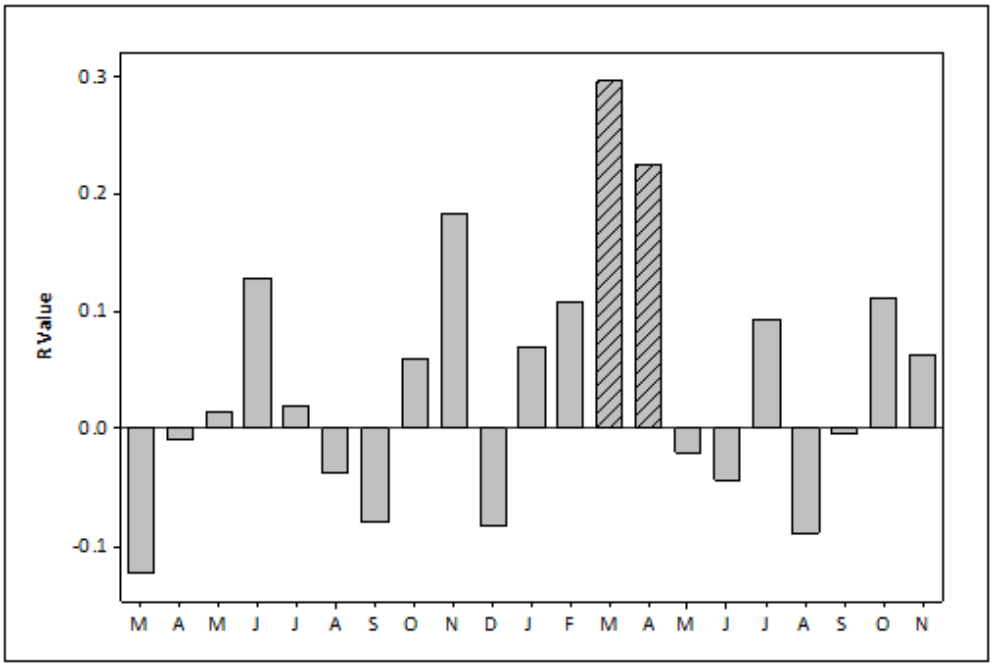

Figure 4.13. Correlation of temperature and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

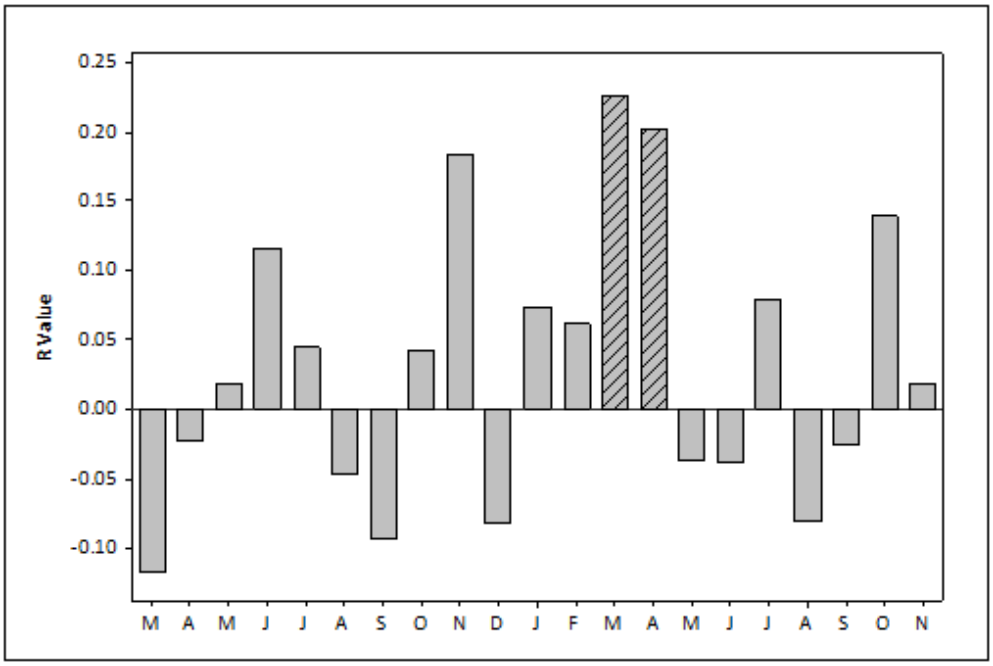

Figure 4.14. Response function of temperature and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

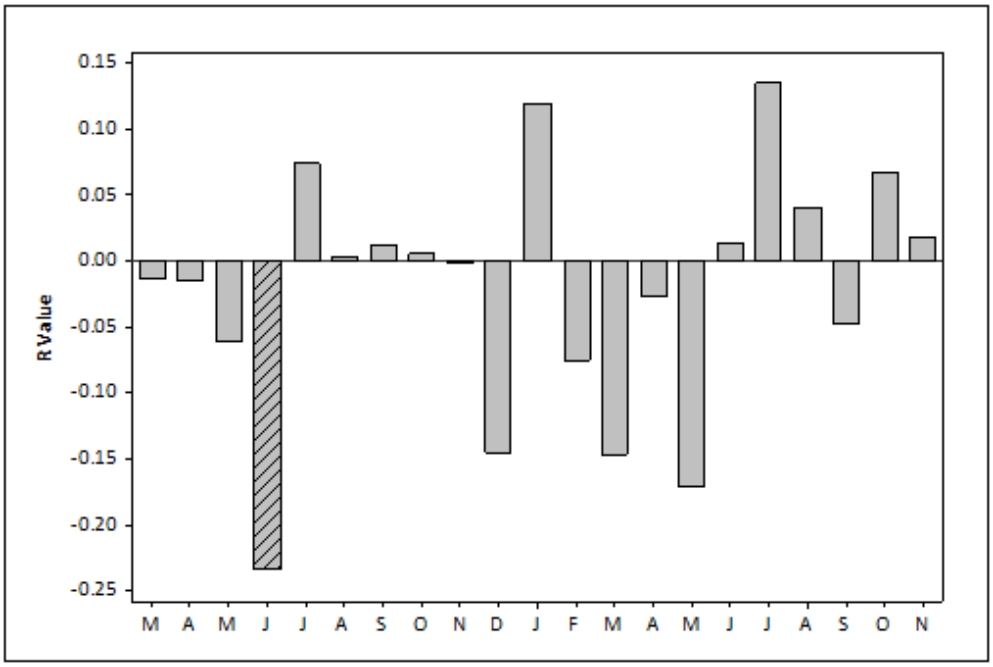

Figure 4.15. Correlation of precipitation and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

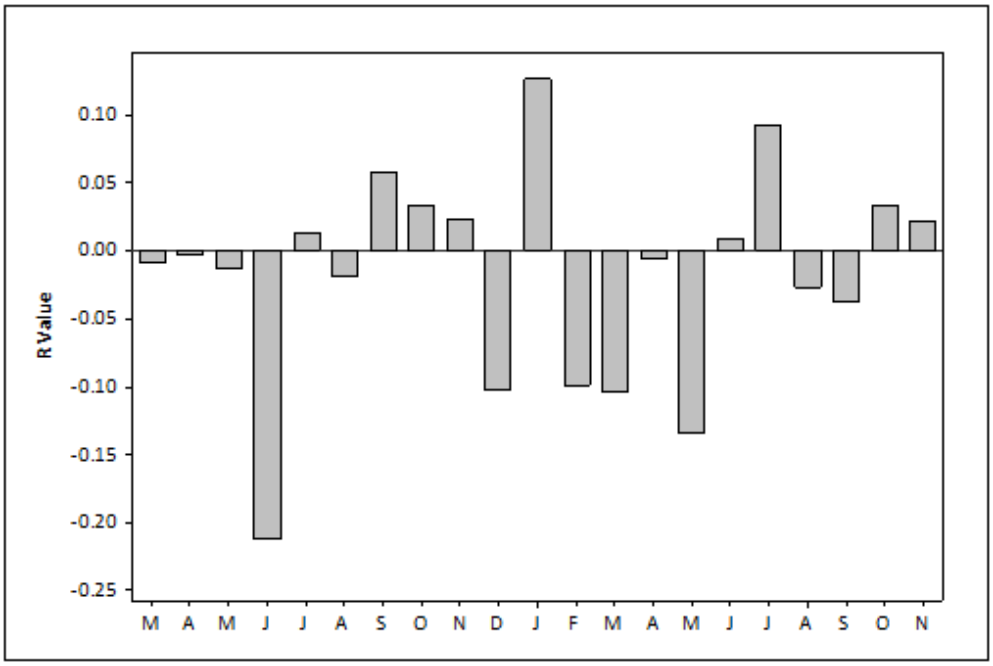

Figure 4.16. Response function of precipitation and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

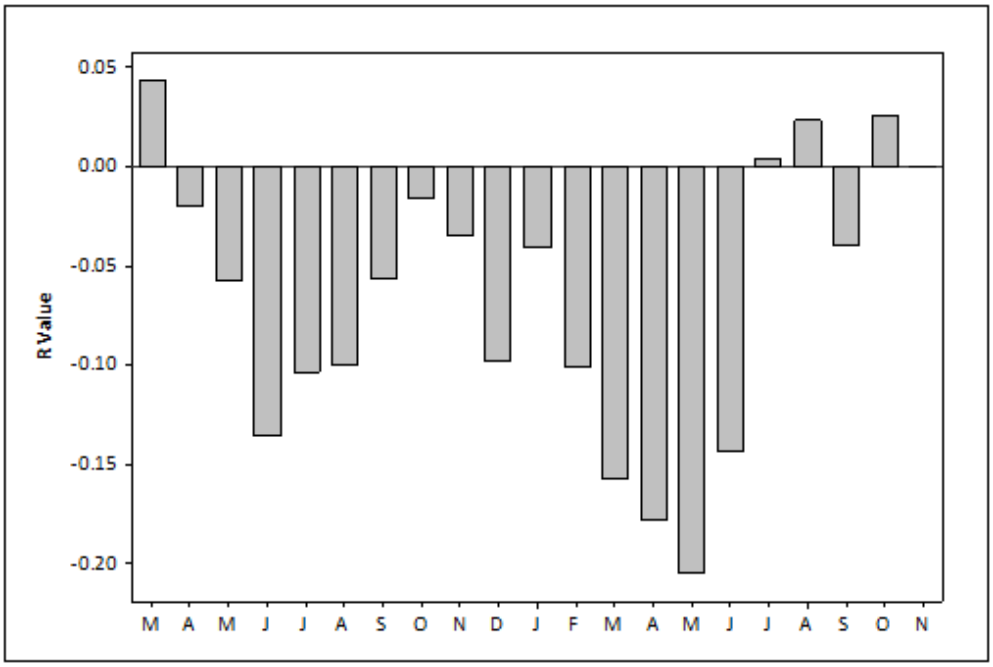

Figure 4.17. Correlation of PDSI and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

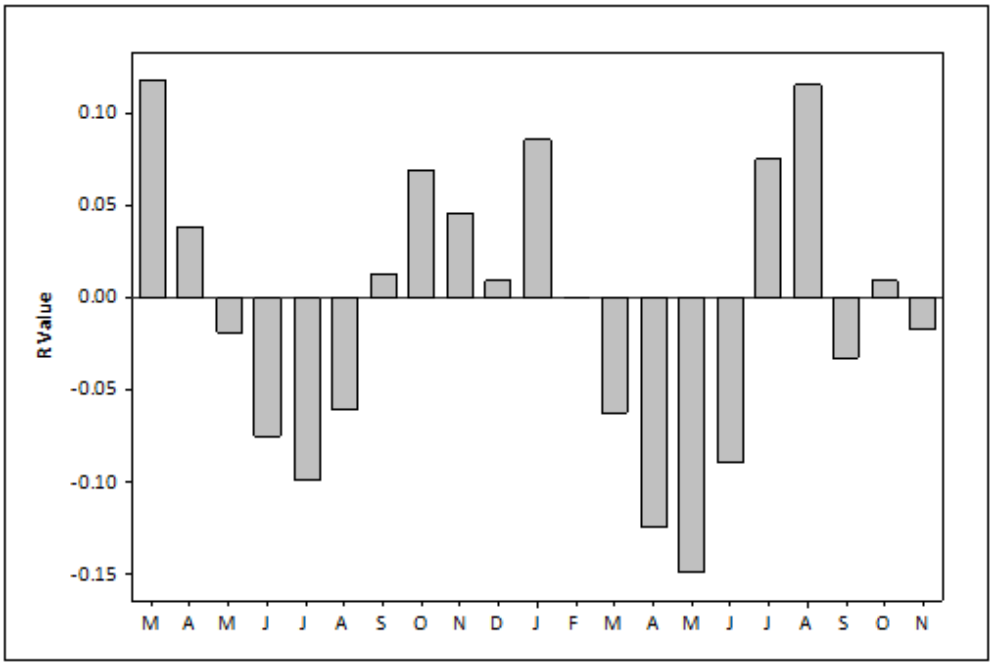

Figure 4.18. Response function of PDSI and growth at mid-elevation site. Hachured bars represent significance, at $p < 0.05$.

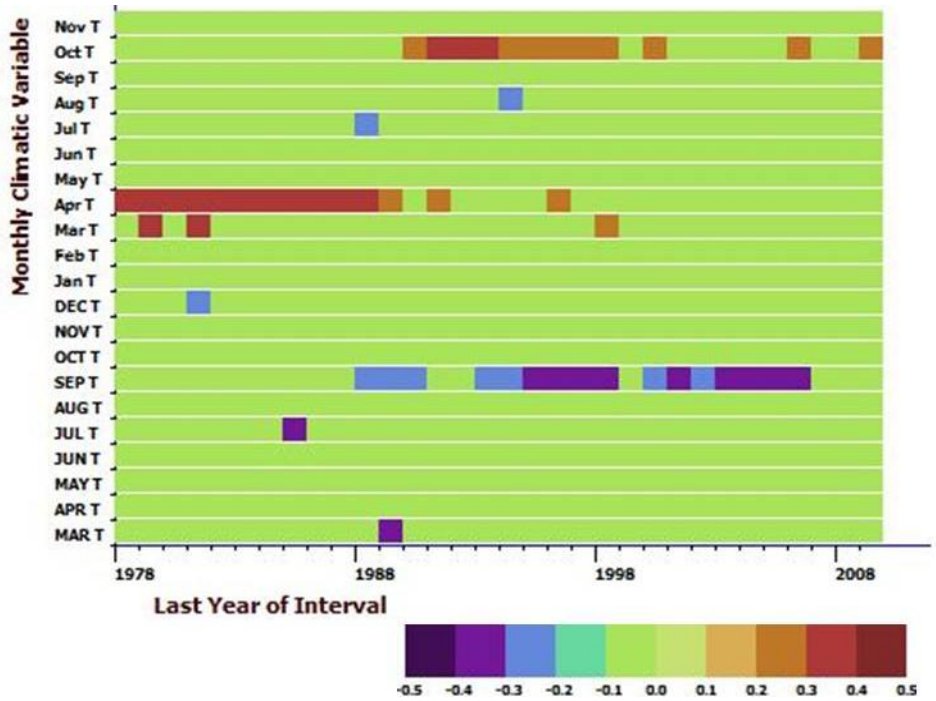

Figure 4.19. Moving correlation of temperature and growth at mid-elevation site.

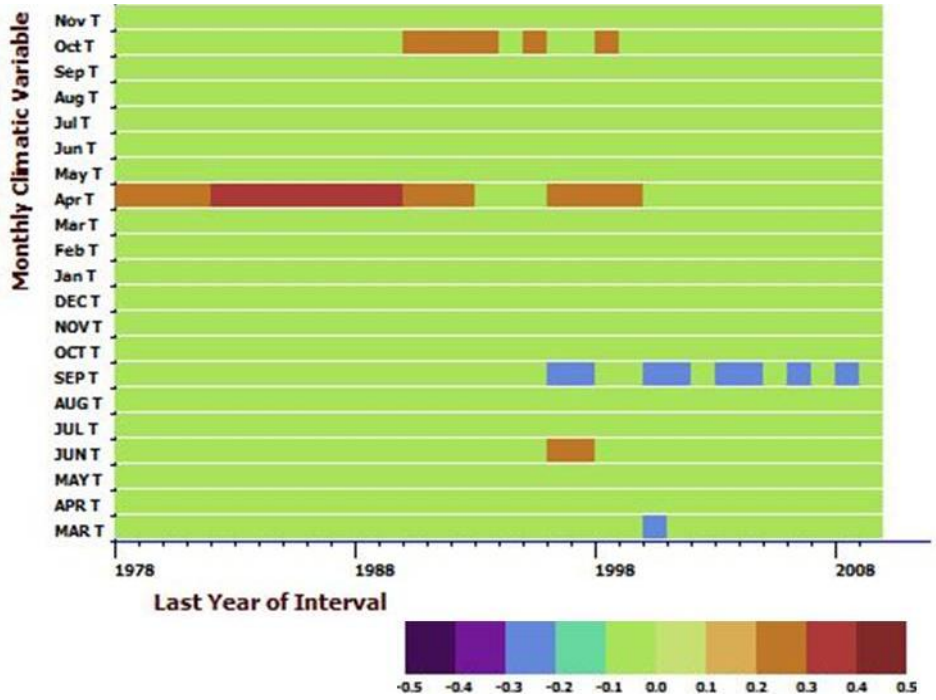

Figure 4.20. Moving response function of temperature and growth at mid-elevation site.

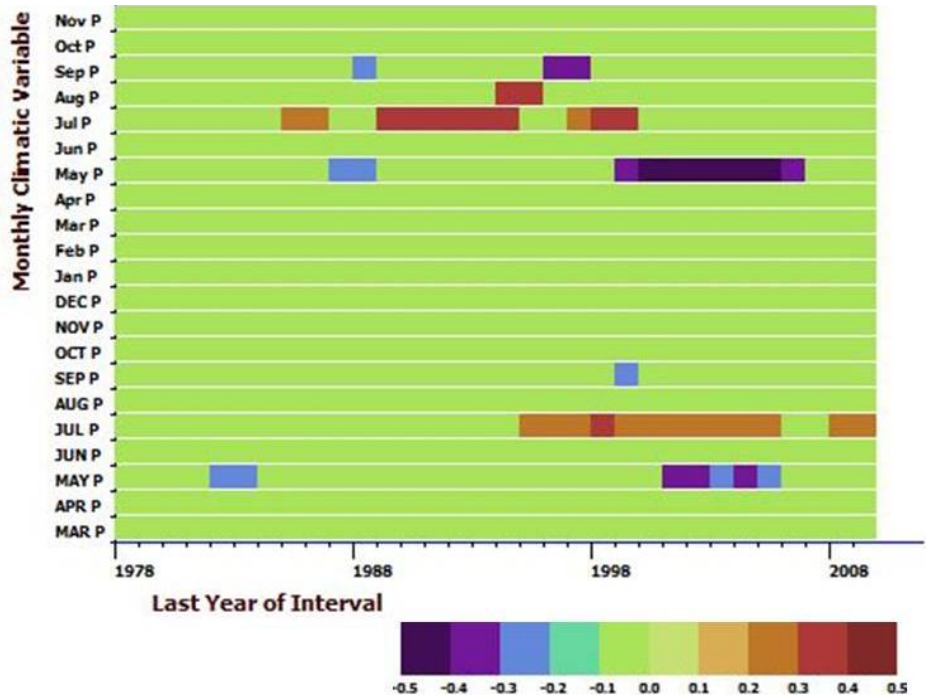

Figure 4.21. Moving correlation of precipitation and growth at mid-elevation site.

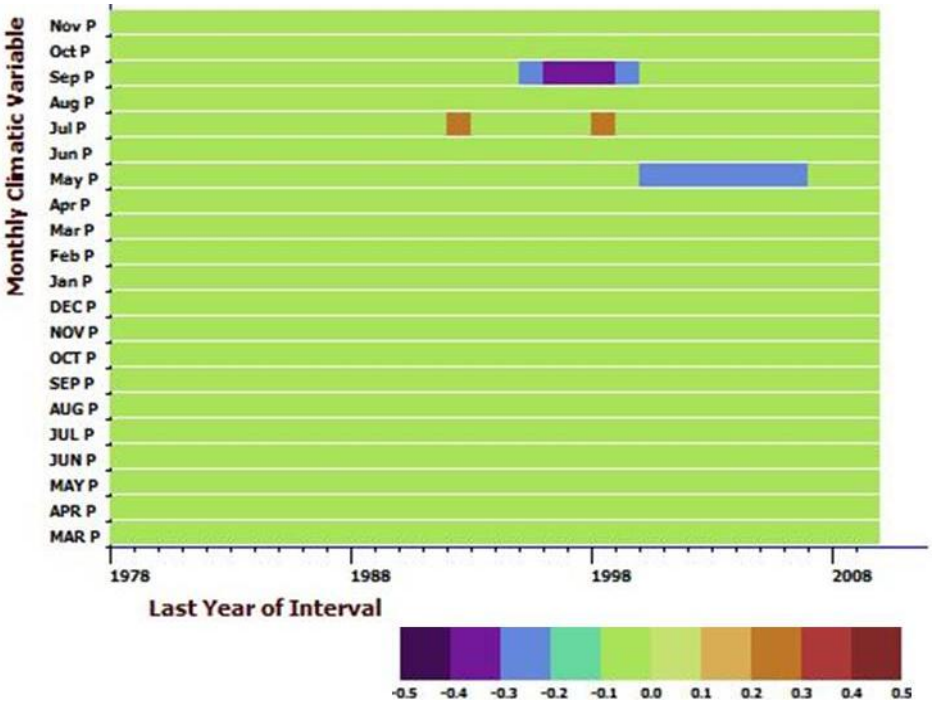

Figure 4.22. Moving response function of precipitation and growth at mid-elevation site.

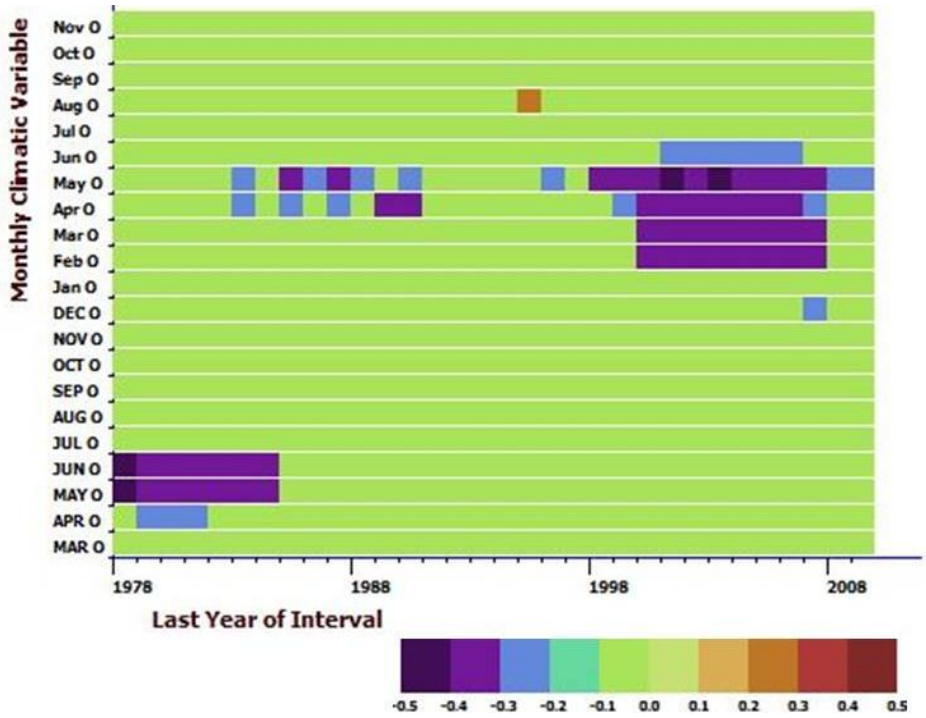

Figure 4.23. Moving correlation of PDSI and growth at mid-elevation site.

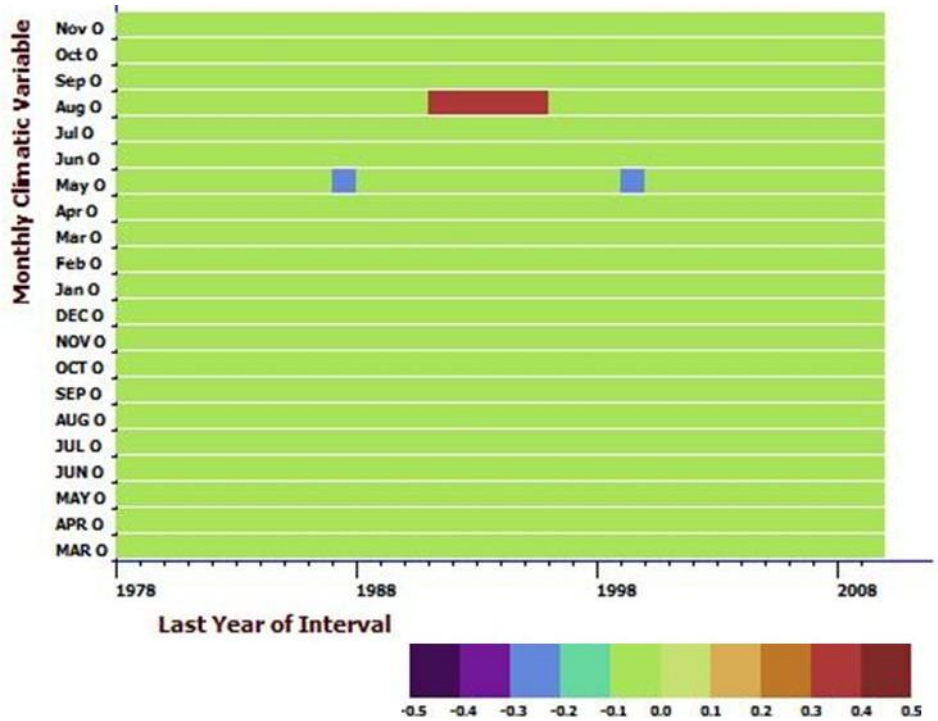

Figure 4.24. Moving response function of PDSI and growth at mid-elevation site.

Linville Mountain, High-Elevation Site

The high-elevation site at Linville Mountain produced 28 series that were successfully cross-dated (Table 4.1). Spanning 91 years, from 1919–2009, this chronology had a mean series length of 62.8 years. Once again, the moderately low inter-series correlation (0.466) and mean sensitivity (0.205) suggest that growth in these specimens is weakly influenced by climate. Nevertheless, dendroclimatological analyses were performed, beginning with the year 1936 to avoid a low expressed population signal (EPS).

At this site, temperature is the only variable determined to be significantly related to growth (Figs. 4.25–4.30). April temperature is positively correlated with growth (r = 0.29; $p < 0.05$), while January temperature is negatively correlated ($r = -0.22$; $p < 0.05$). According to the response function analysis, only April temperature significantly impacts growth.

Moving interval analysis revealed that the role of April temperature has decreased in recent decades, while November temperature has become more important (Figure 4.31). Surprisingly, November temperature is negatively correlated with growth, and this holds up even under the statistical scrutiny of the response function analysis (Figure 4.32). Other notable relationships include negative correlations of growth with January and previous November temperature. Neither of these relationships has been significant in recent years.

Though precipitation was not correlated with growth when considering the entire chronology, the moving correlation function did yield significant results (Figs. 4.33). A

formerly significant, negative effect of previous November precipitation has given way to a negative correlation between February precipitation and radial growth. In moving response function analysis (Figure 4.34), the role of November precipitation was statistically insignificant, while February precipitation remained so.

Early in the chronology, PDSI—of both the previous and current summers—had an inverse correlation with growth (Figure 4.35). More recently, growth has demonstrated no notable correlation with PDSI. Once again, because of response functions' treatment of collinear independent variables, the moving response function indicated that essentially no monthly PDSI significantly correlated with growth for any length of time (Figure 4.36).

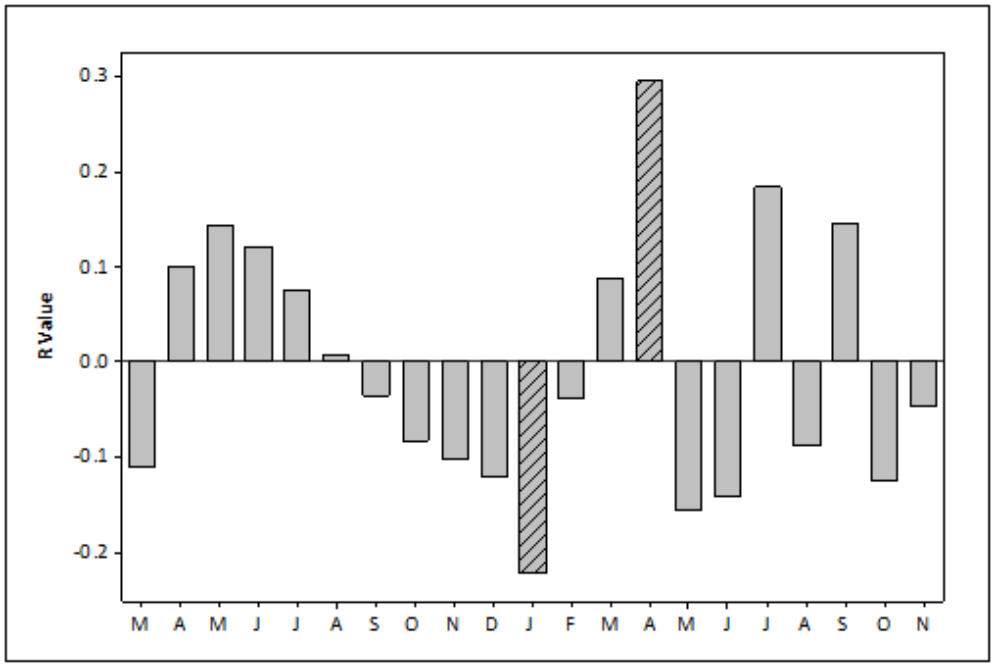

Figure 4.25. Correlation of temperature and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

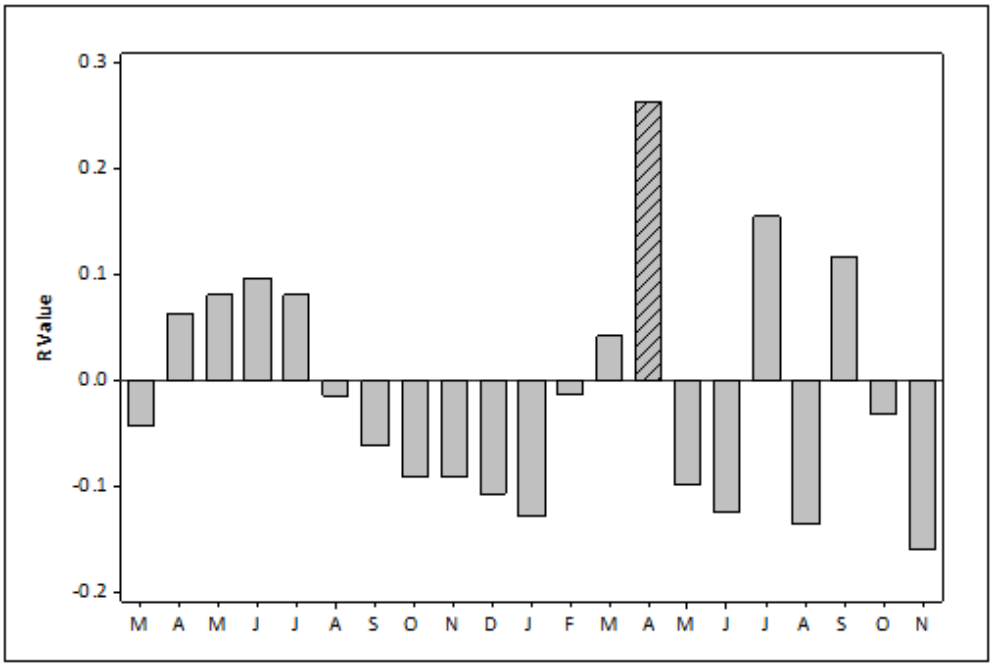

Figure 4.26. Response function of temperature and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

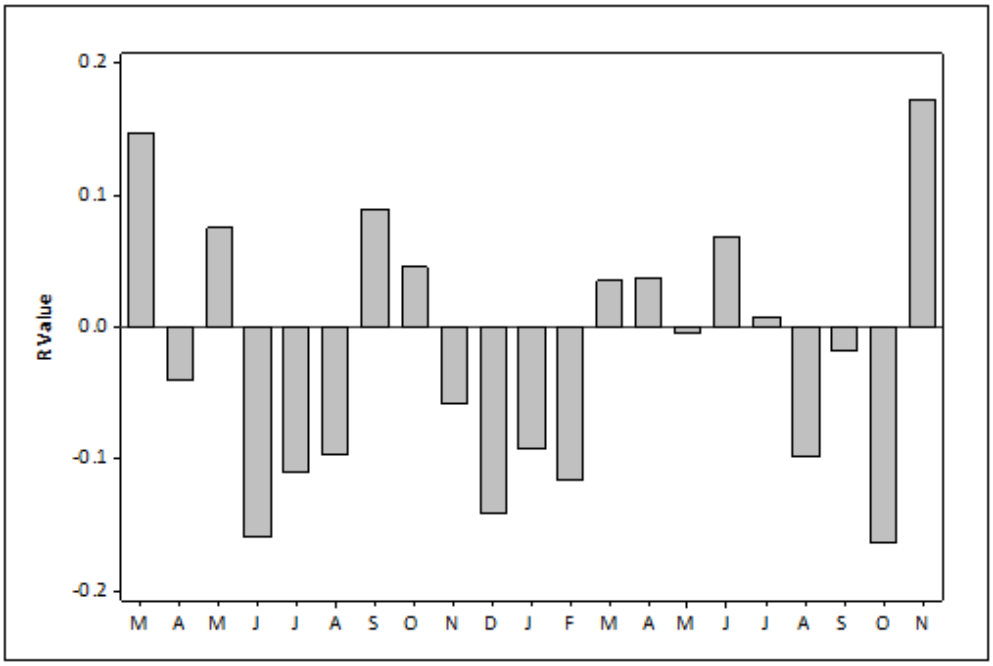

Figure 4.27. Correlation of precipitation and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

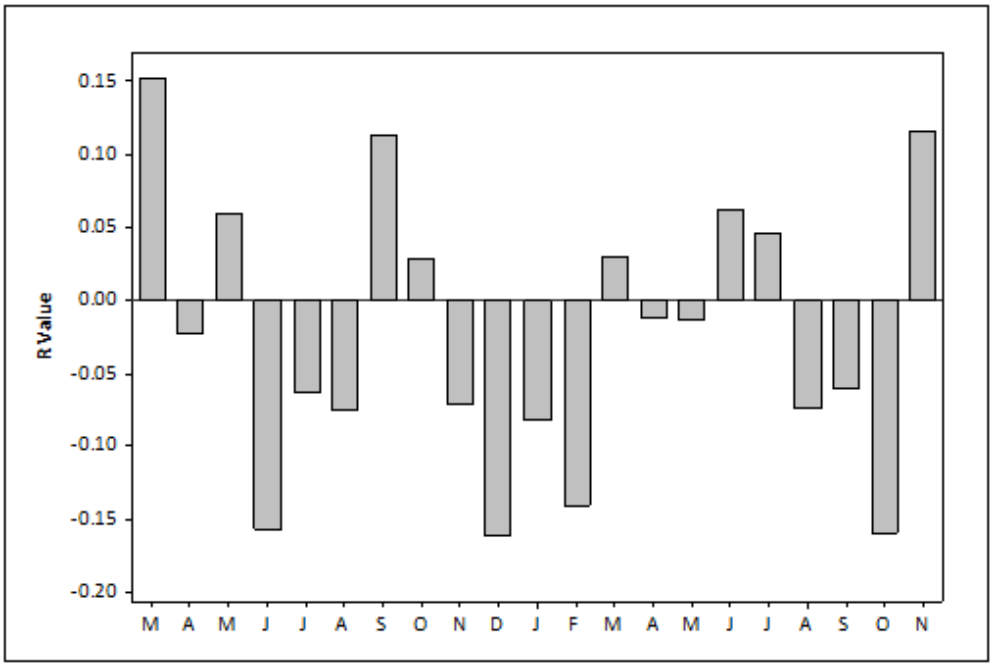

Figure 4.28. Response function of precipitation and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

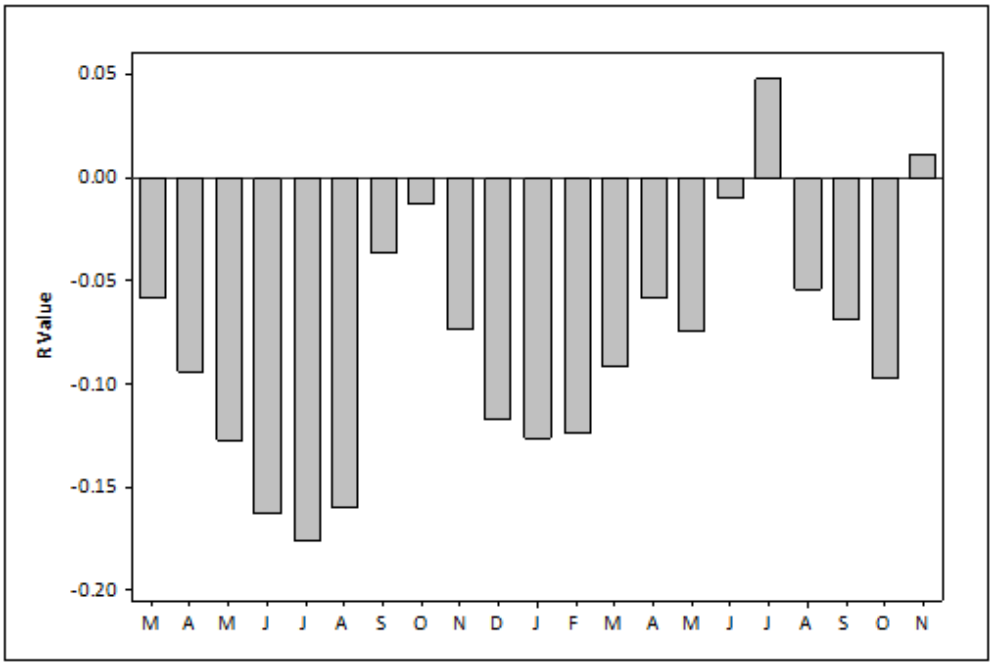

Figure 4.29. Correlation of PDSI and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

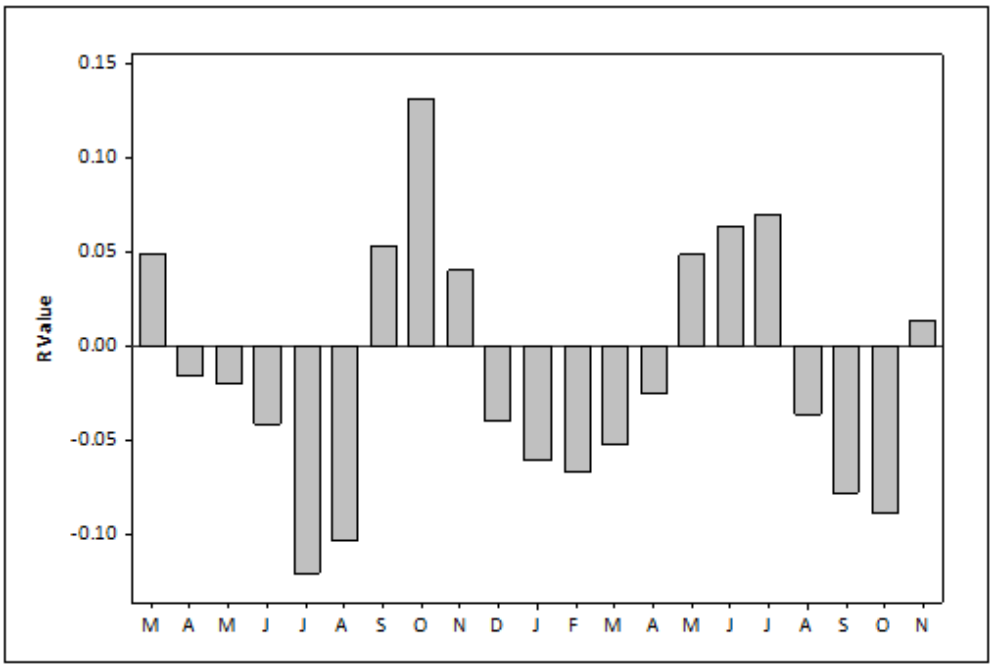

Figure 4.30. Response function of PDSI and growth at high-elevation site. Hachured bars represent significance, at $p < 0.05$.

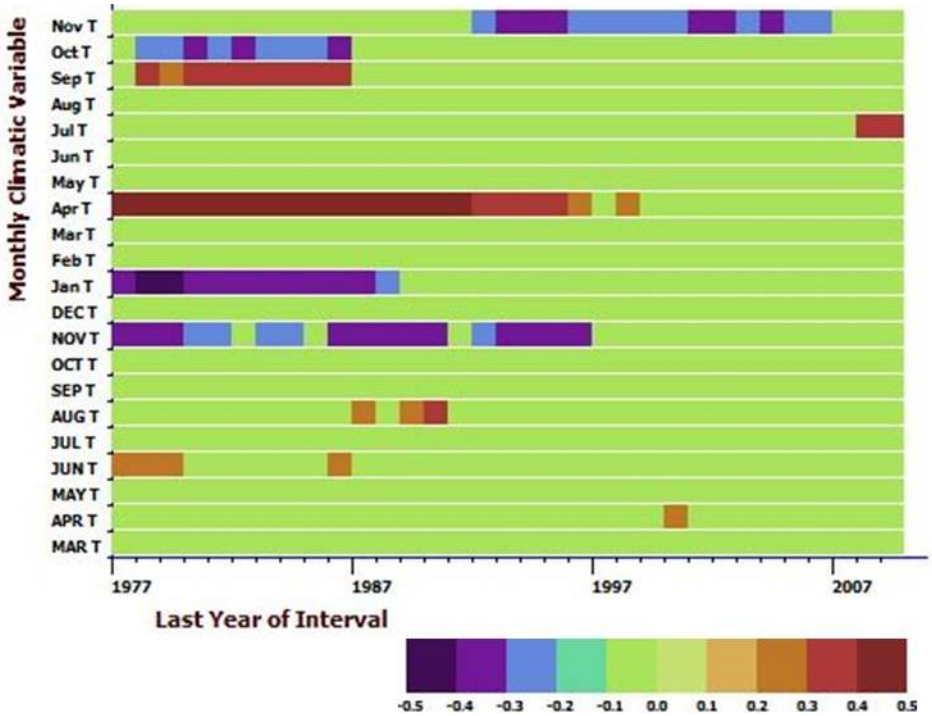

Figure 4.31. Moving correlation of temperature and growth at high-elevation site.

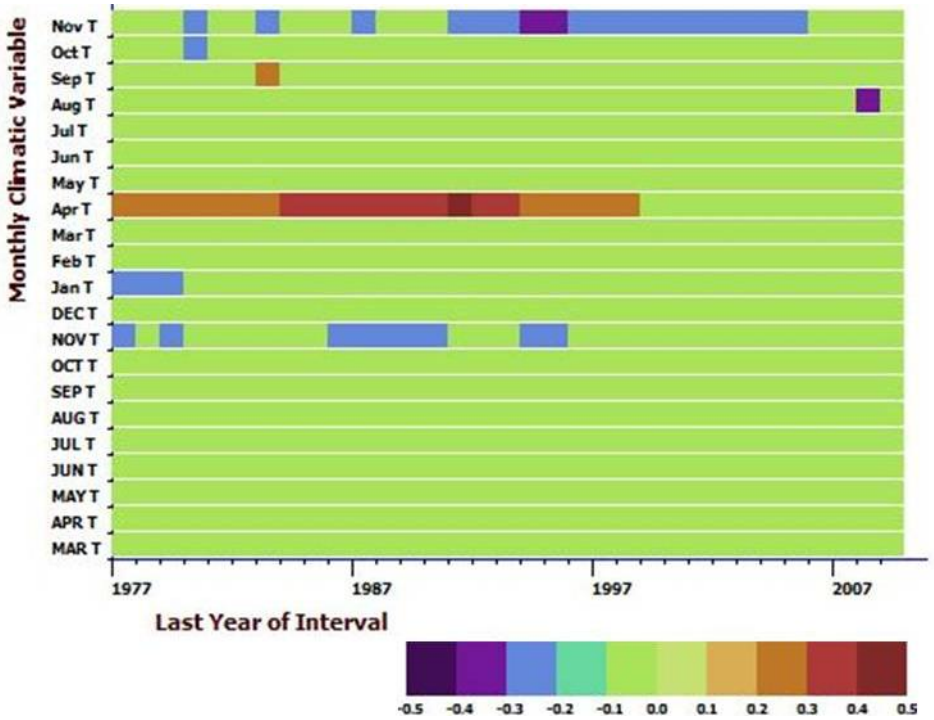

Figure 4.32. Moving response function of temperature and growth at high-elevation site.

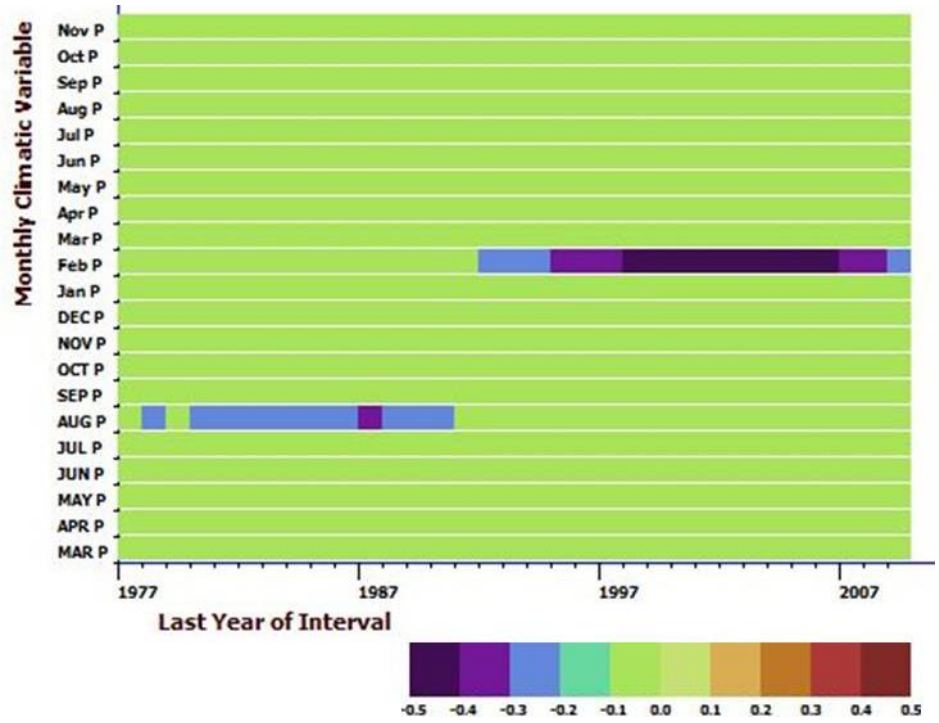

Figure 4.33. Moving correlation of precipitation and growth at high-elevation site.

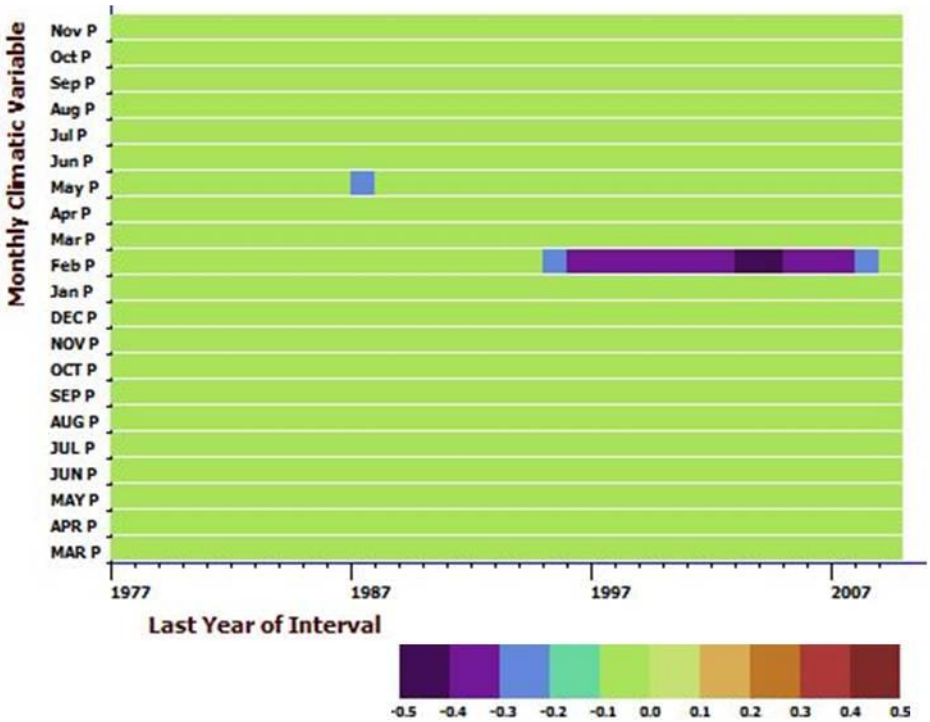

Figure 4.34. Moving response function of precipitation and growth at high-elevation site.

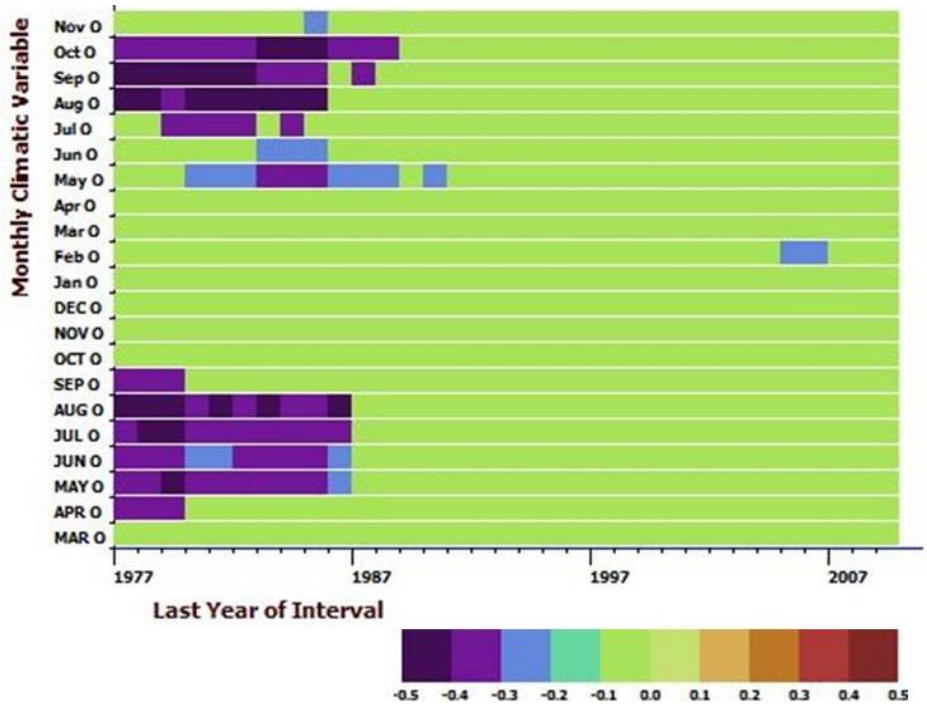

Figure 4.35. Moving correlation of PDSI and growth at high-elevation site.

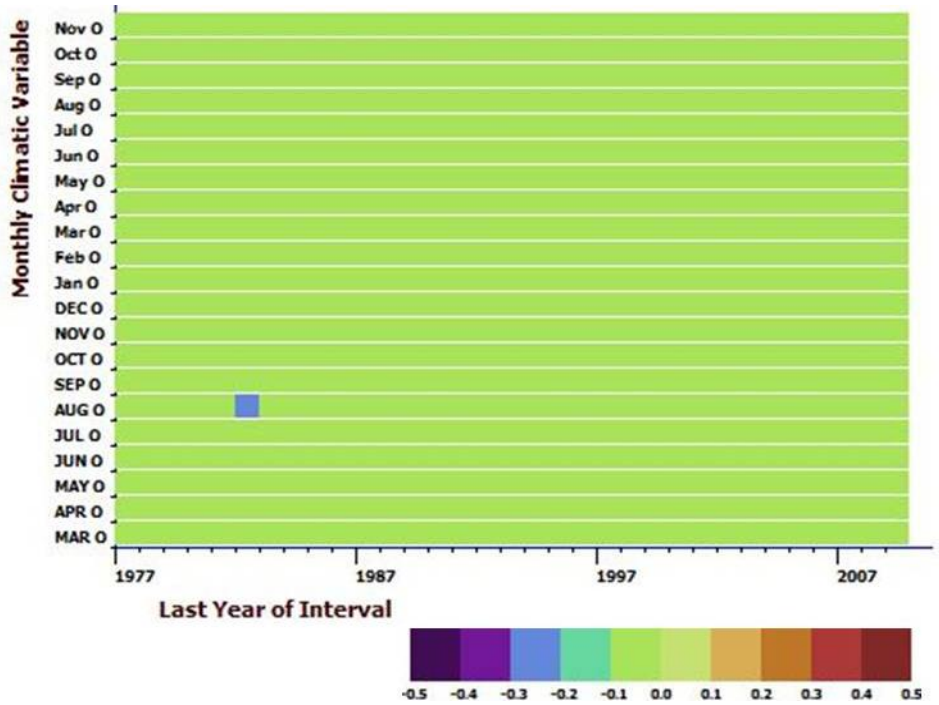

Figure 4.36. Moving response function of PDSI and growth at high-elevation site.

White Pines Preserve

The chronology from White Pines Preserve dated from 1848–2009. At 162 years, it is the oldest of the four chronologies. The 31 cross-dated series have a mean length of 76.1 years. This site also has the highest inter-series correlation, at 0.611. The mean sensitivity is 0.218. The time-frame used in analysis was limited only by the availability of reliable meteorological records, which began in 1895.

The trees at this site reveal significant correlations with temperature during ten of the twenty-one months examined (Figure 4.37). Like the other sites, growth was positively correlated with spring temperature, in this case during the month of March (r = 0.24; $p < 0.05$). Temperature during the summer months, of both the previous and current years, is inversely correlated with growth. As expected, the current summer

demonstrates a stronger effect on growth than the previous summer, with the current August displaying the strongest correlation ($r = -0.33$; $p < 0.05$). Warm Decembers are also associated with restricted growth ($r = -0.22$; $p < 0.05$). In response function analysis, only two of these ten relationships remain significant: December ($r = -0.15$; $p < 0.05$) and August ($r = -0.20$; $p < 0.05$) temperature (Figure 4.38).

May and July precipitation are significantly, positively related to growth, according to both the correlation and response functions (Figure 4.39 and 4.40). PDSI is also positively correlated with growth, from May through November, with *r* values as high as 0.45 (Figure 4.41). The seven month persistence of this correlation is probably related to the autocorrelation inherent in PDSI (Palmer, 1965). This interpretation is supported by the fact that the response function analysis determined PDSI only to be significant in the months of July and August (Figure 4.42).

Moving correlation analysis revealed that March temperature has had the most consistent effect on growth, though it has been substituted by February temperature in recent years (Figure 4.43). Current summer temperatures have only become a limiting factor for radial growth during the latter half of the chronology. Even under the highly selective moving response functions, February temperature and August temperature correlate with growth toward the end of the chronology (Figure 4.44).

According to the moving correlation function of precipitation data, no monthly variable has had a persistent impact on growth (Figure 4.45). Precipitation during May, June, and July have exhibited intermittent, positive correlations with growth, especially in the most recent years. The response functions revealed no notable results (Figure 4.46).

Combining the effects of antecedent temperature and precipitation, PDSI had the most pervasive effect on growth during the summer and fall, but only in the early decades of the chronology (Figure 4.47). Recently, PDSI of the summer months has once again become a significant factor in radial growth. Also recently emerging as a factor in growth is the summer PDSI of the previous year. Though present in the correlation functions, neither of these recent shifts is evident in the moving response functions (4.48).

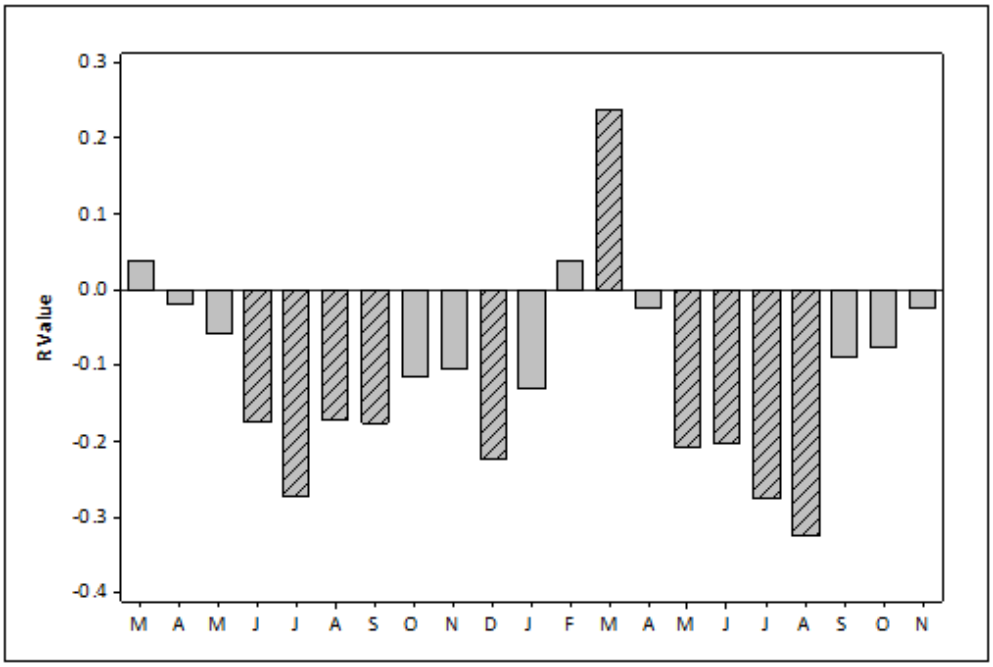

Figure 4.37. Correlation of temperature and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

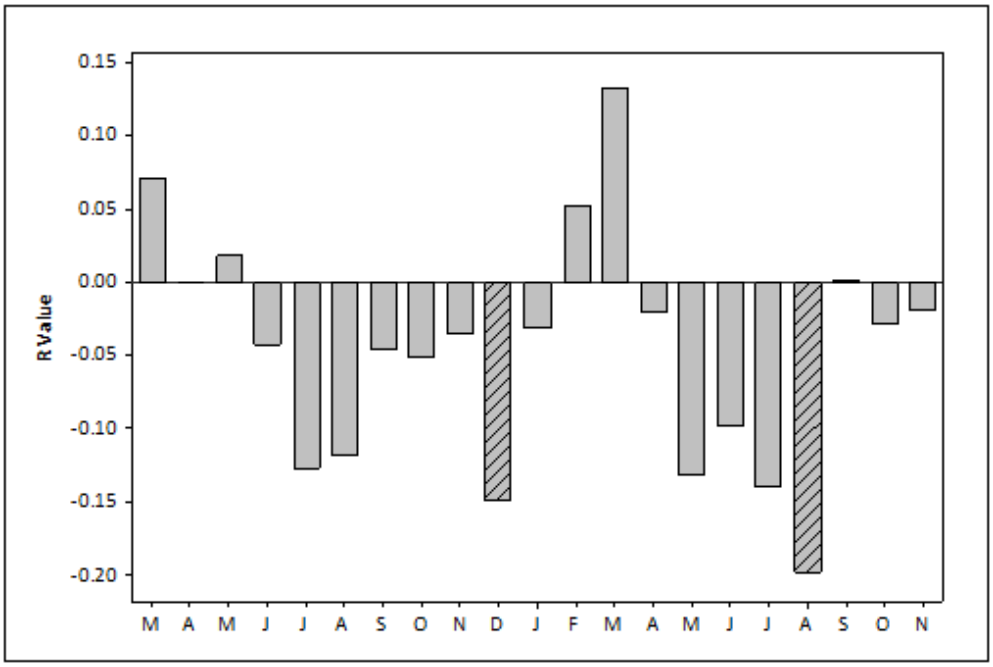

Figure 4.38. Response function of temperature and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

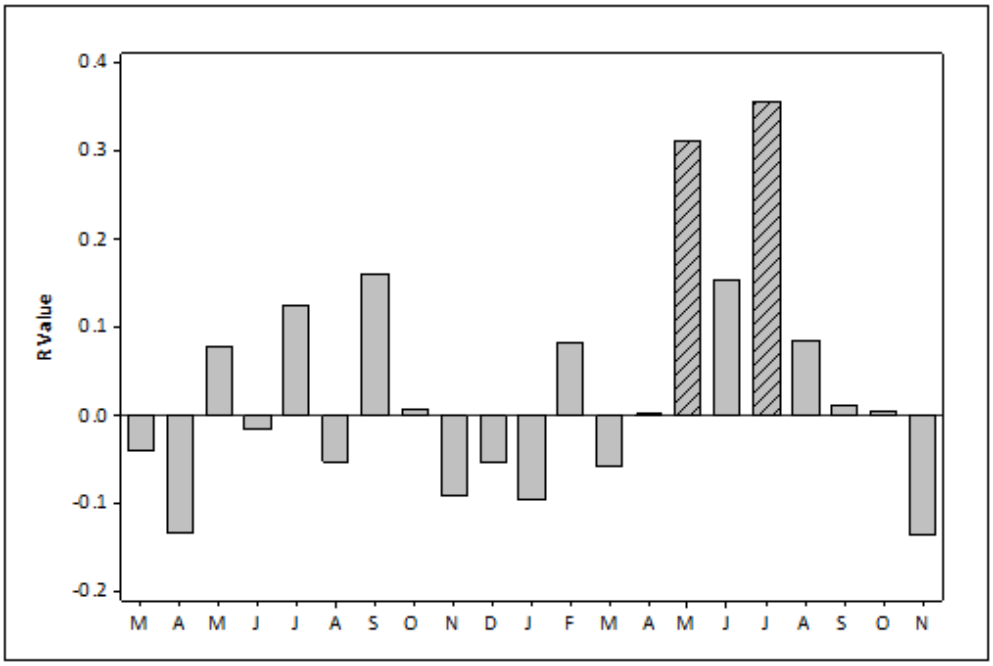

Figure 4.39. Correlation of precipitation and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

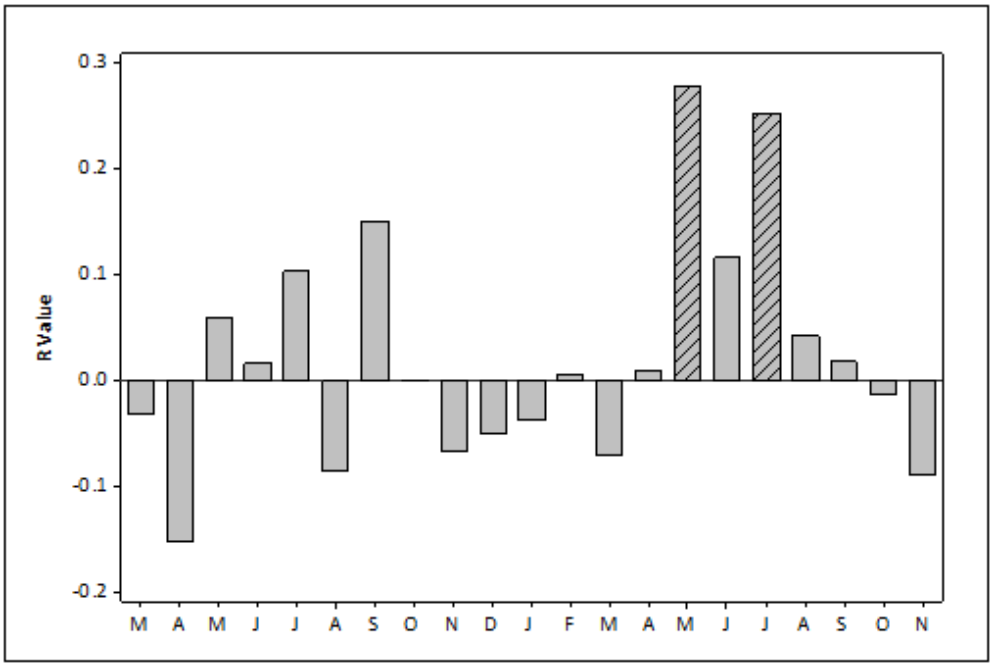

Figure 4.40. Response function of precipitation and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

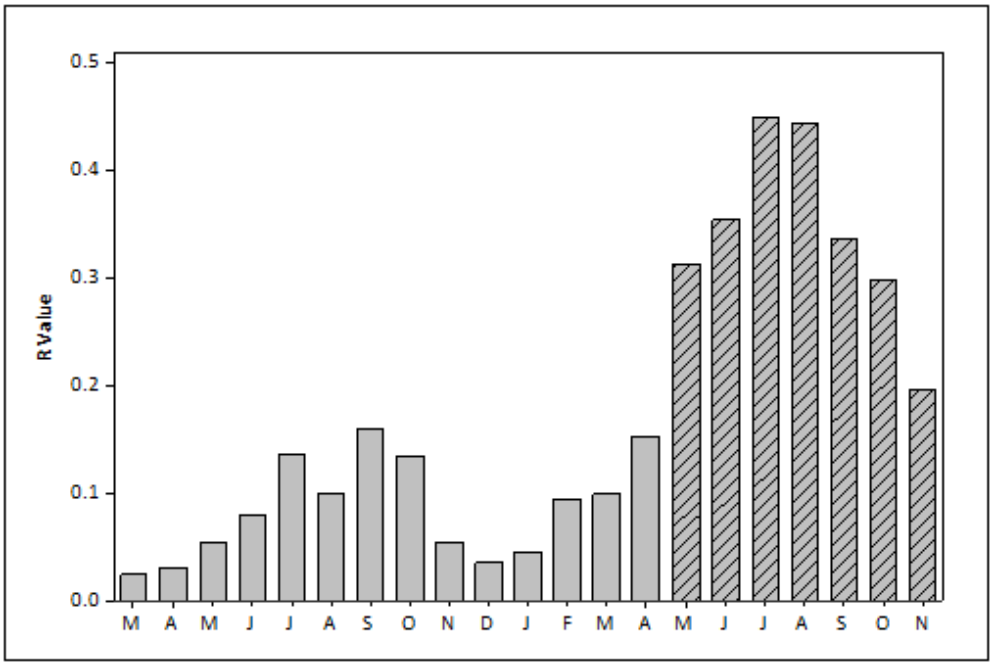

Figure 4.41. Correlation of PDSI and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

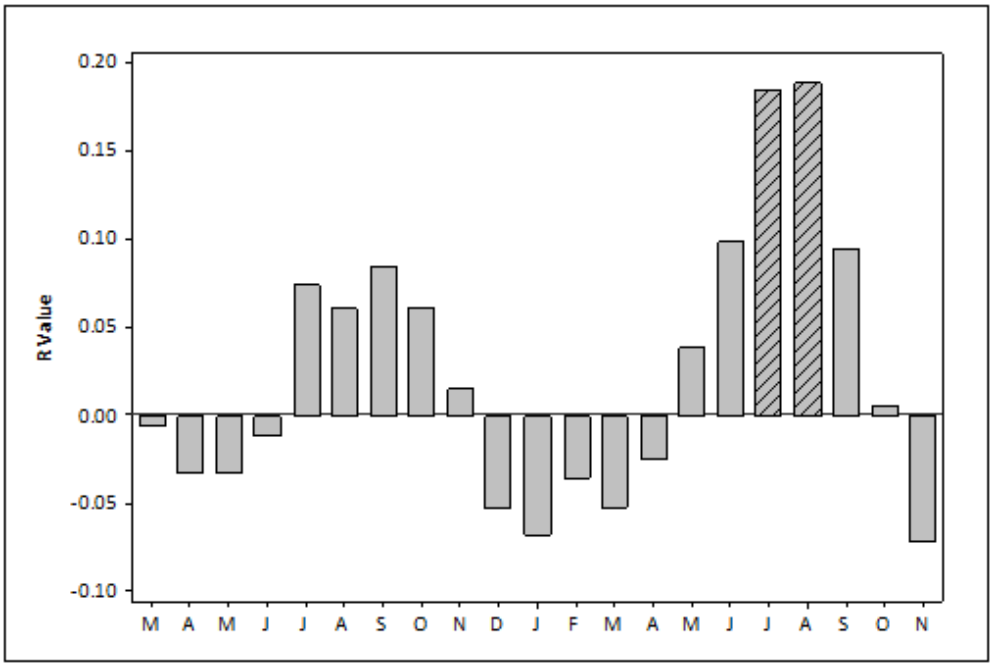

Figure 4.42. Response function of PDSI and growth at White Pines Preserve. Hachured bars represent significance, at $p < 0.05$.

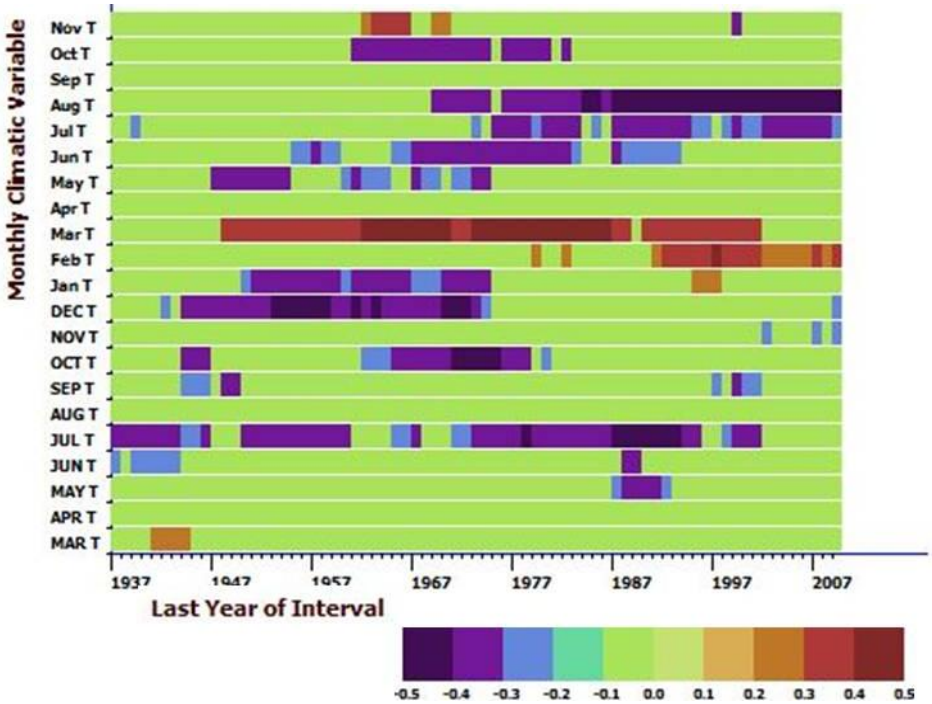

Figure 4.43. Moving correlation of temperature and growth at White Pines Preserve.

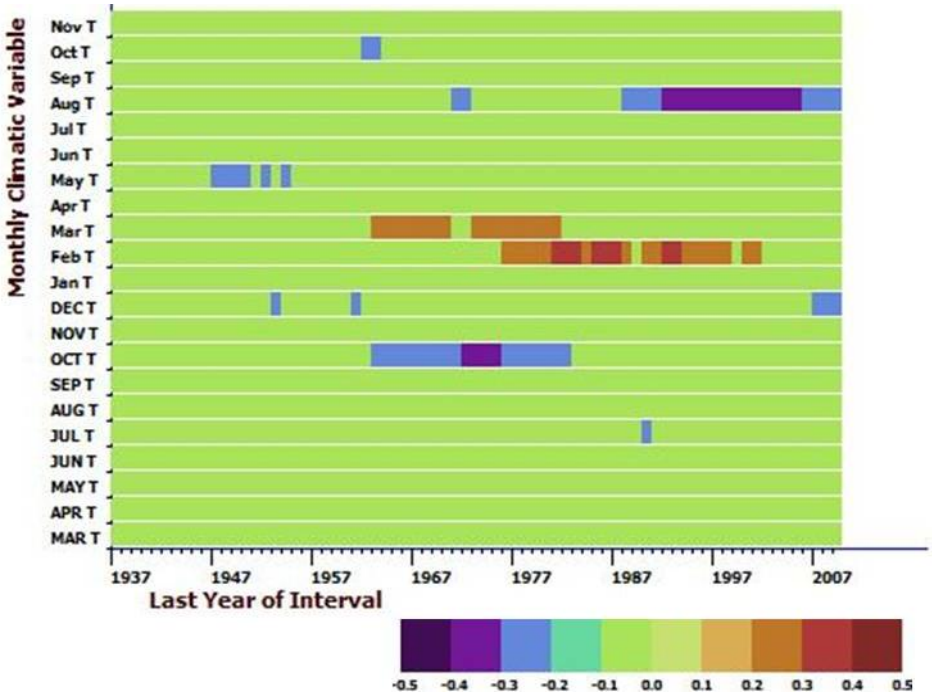

Figure 4.44. Moving response function of temperature and growth at White Pines Preserve.

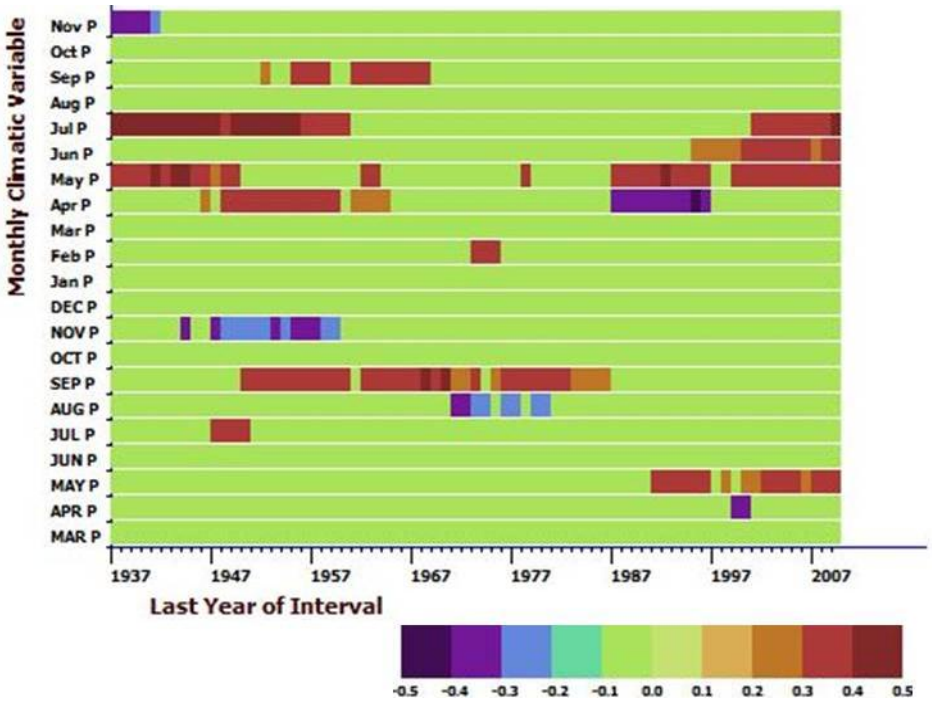

Figure 4.45. Moving correlation of precipitation and growth at White Pines Preserve.

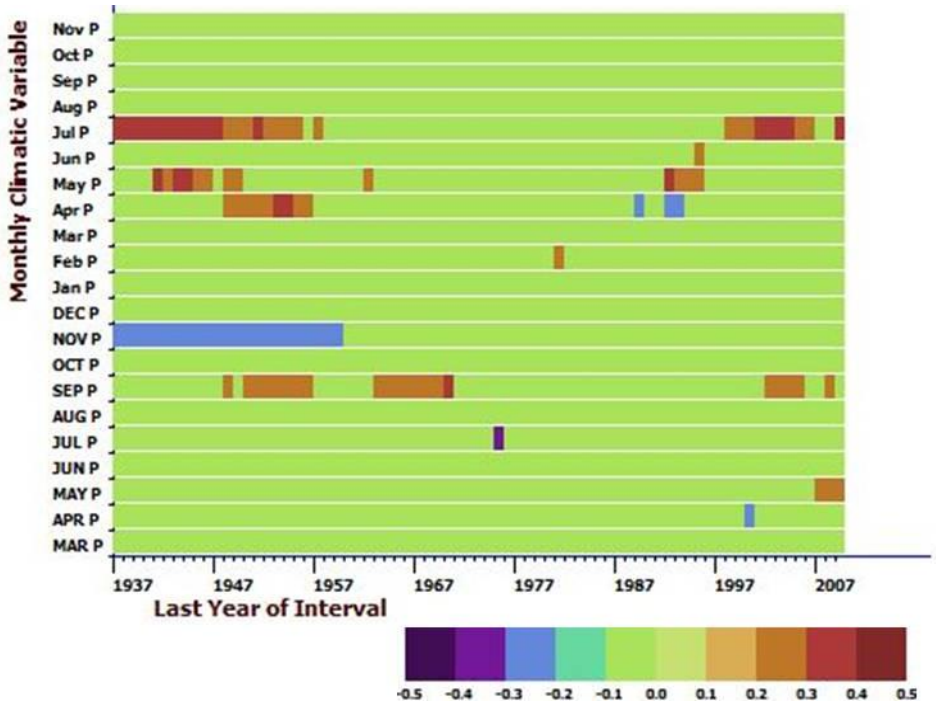

Figure 4.46. Moving response function of precipitation and growth at White Pines Preserve.

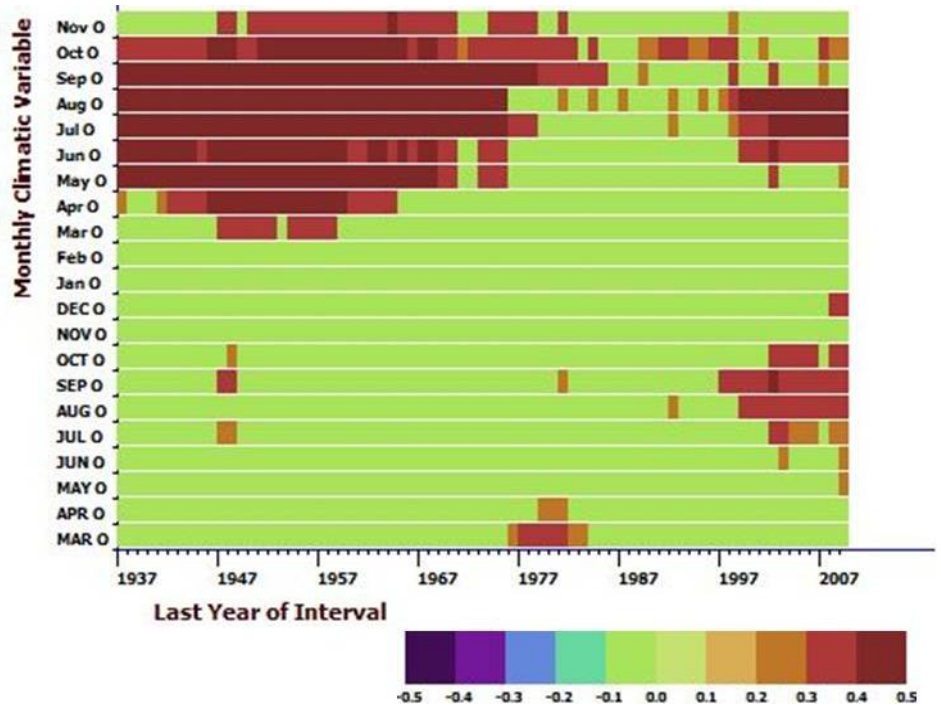

Figure 4.47. Moving correlation of PDSI and growth at White Pines Preserve.

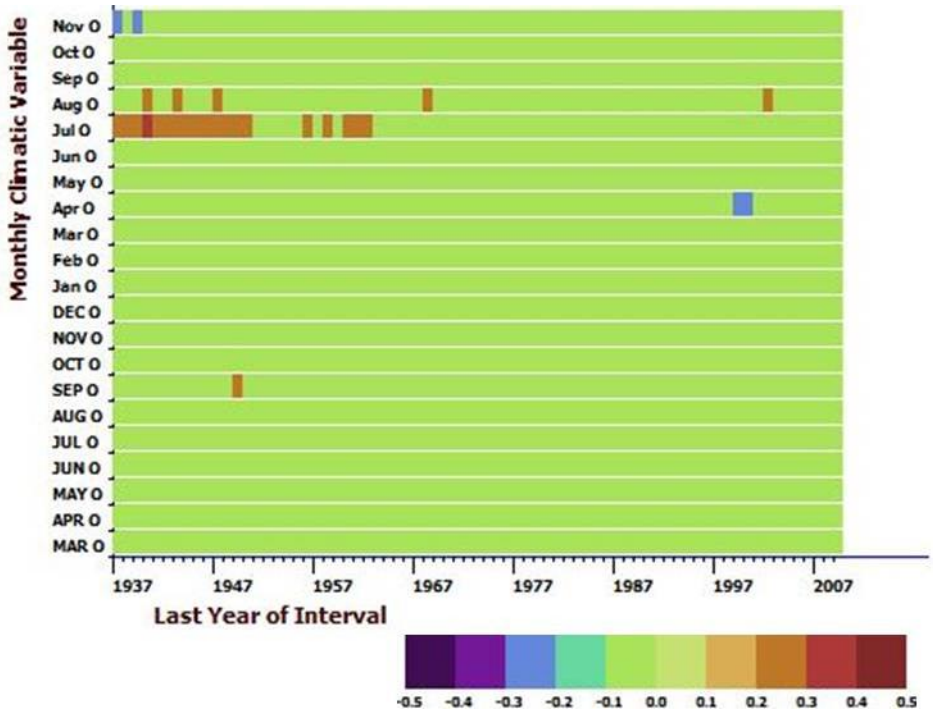

Figure 4.48. Moving response function of PDSI and growth at White Pines Preserve.

Mean Sensitivity

Local Factors

Of the 25 sets of correlations calculated between mean sensitivity and topographic factors, only one was statistically significant (Table 4.2). At the high-elevation site on Linville Mountain, the coarse resolution, LANDFIRE-interpolated slope was correlated with mean sensitivity at $r = -0.631$ ($p = 0.007$). Contrary to the suggestions of Fritts (1976), this indicates that more complacent trees are found on steeper surfaces. However, due to multiple comparisons, the Bonferroni correction is necessary to reduce the risk of type I error (Dunn, 1961). The adjusted significance level becomes 0.002, in which case, this relationship is insignificant. The fact that none of the examined

topographic factors influences mean sensitivity lends credence to a broader interpretation of the statistic than is usually applied.

Variable	High Elevation	Mid Elevation	Low Elevation	White Pines Preserve	All Sites
Slope	0.31	-0.02	0.3	0.1	0.14
Southern Exposure	0.07	-0.47	-0.24	-0.01	0.01
Elevation (LANDFIRE)	0.2	0.22	0.18	-0.22	-0.21
Slope (LANDFIRE)	-0.63*	-0.02	0.29	0.1	-0.19
Southern Exposure (LANDFIRE)	0.14	-0.06	-0.02	0.22	0.08

Table 4.2. Correlation coefficients for topographic site factors and mean sensitivity of individual trees. Those marked with an asterisk are statistically significant ($p < 0.05$) prior to applying the Bonferroni correction.

Geographic Patterns

Values of mean sensitivity ranged from 0.15, at Westward Lake, near Ottawa, to 0.31, at Turtle Lake in southwestern Ontario (Figure 4.49). The mean was 0.22, with a standard deviation of 0.03. Though these rank from low to moderate on the scale of global values of mean sensitivity (Fritts, 1976; Falcon-Lang, 2005), for the purposes of this study, what matters most is the relative values within a given species. The correlation analysis confirmed the hypothesis that mean sensitivity increases toward the edge of a species' geographic distribution. Distance to the range edge was correlated to

mean sensitivity at $r = -0.647$ ($p < 0.001$). This correlation withstands the Bonferroni correction, which lowers the significance level to 0.01. Given that this pattern corresponds with that expected for climatic response under traditional theories of range dynamics and optimum response surfaces (Hutchins, 1947; Hengeveld, 1990; Brown, 1995; Gaston, 2003), this result validates the application of mean sensitivity in examinations of macroclimatic tolerance.

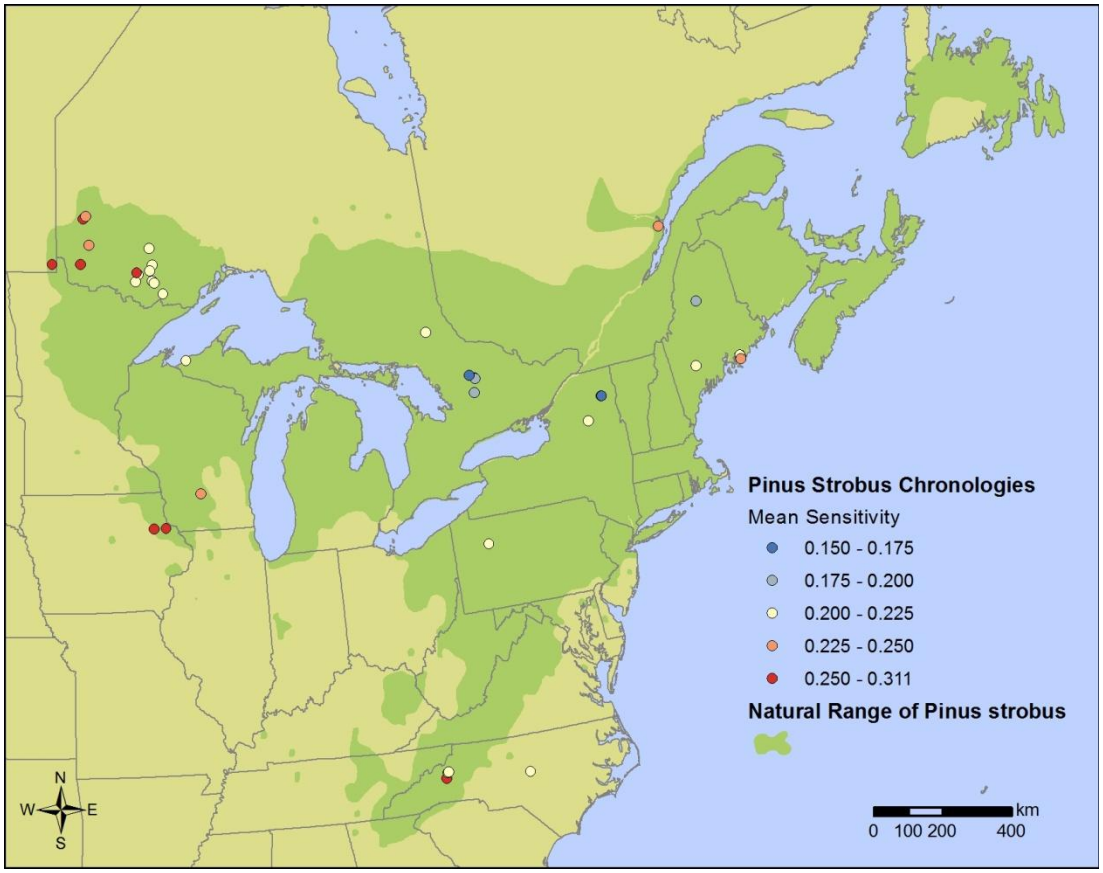

Figure 4.49. Map of *P. strobus* chronologies. Chronologies symbolized according to value of mean sensitivity.

Longitude was also significantly, inversely correlated to mean sensitivity ($r = -0.466$; $p < 0.005$), indicating that sensitivity is higher to the west. The longitudinal

gradient is misleading, however. In the east of its range, *P. strobus* migration is limited by the presence of the Atlantic Ocean rather than by climate. Because the species' climatic center—though not its geographic center—is near the coast, and its distribution is prevented from advancing eastward, the longitudinal trend is probably related to moisture or to some other climatic variable. Indeed, mean sensitivity's correlation with annual precipitation was nearly significant ($r = -0.306$; $p = 0.065$). Though this correlation is low and statistically insignificant, the combination of these results suggests that moisture plays an important role throughout *P. strobus*' range. None of the remaining geographic factors—mean annual temperature, elevation, or latitude—was determined to be significantly correlated to mean sensitivity.

Global Regression

The global OLS regression with mean sensitivity as the dependent variable resulted in a formula of

$$MS = 0.290116 + -0.000098x + 0.004752y,$$

where x is the annual precipitation and y is the annual mean temperature. Both of the coefficients and the intercept were significant at $p < 0.01$. The Variance Inflation Factor (VIF) was 2.3, indicating that multicollinearity was not an issue with the selected independent variables. The R^2 was 0.213, with an adjusted R^2 of 0.166. The AICc was equal to −150.1, but this value only has meaning in comparison to another model for the same dependent variable (Fotheringham et al., 2002). The Jarque-Bera statistic was not

significant, indicating that the residuals were normally distributed (Jarque and Bera, 1980). The Koenker (BP) statistic was not significant either, which suggests stationarity of the processes in geographic space and homoscedasticity in data space (Koenker, 1981; ESRI, 2009). With an insignificant Koenker (BP) statistic, the *F*-statistic becomes a valid assessment of overall model significance. In this case, a joint *F*-statistic of 4.59, with a $p < 0.05$, indicates a significant model.

Despite the indication of stationarity by the Koenker (BP) test, a map of the residuals (Figure 4.50) suggested that they were clustered. I further tested for non-stationarity by calculating Moran's *I* for the residuals. Indeed, with a 400 km distance band defining adjacency, the resulting Moran's *I* of 0.12 was significant, with a *p*-value of 0.02. The positive value of Moran's *I* indicates spatial clustering of the residuals. This suggests that the model could be improved by implementing the same variables in a geographically weighted regression (Zhang et al., 2005).

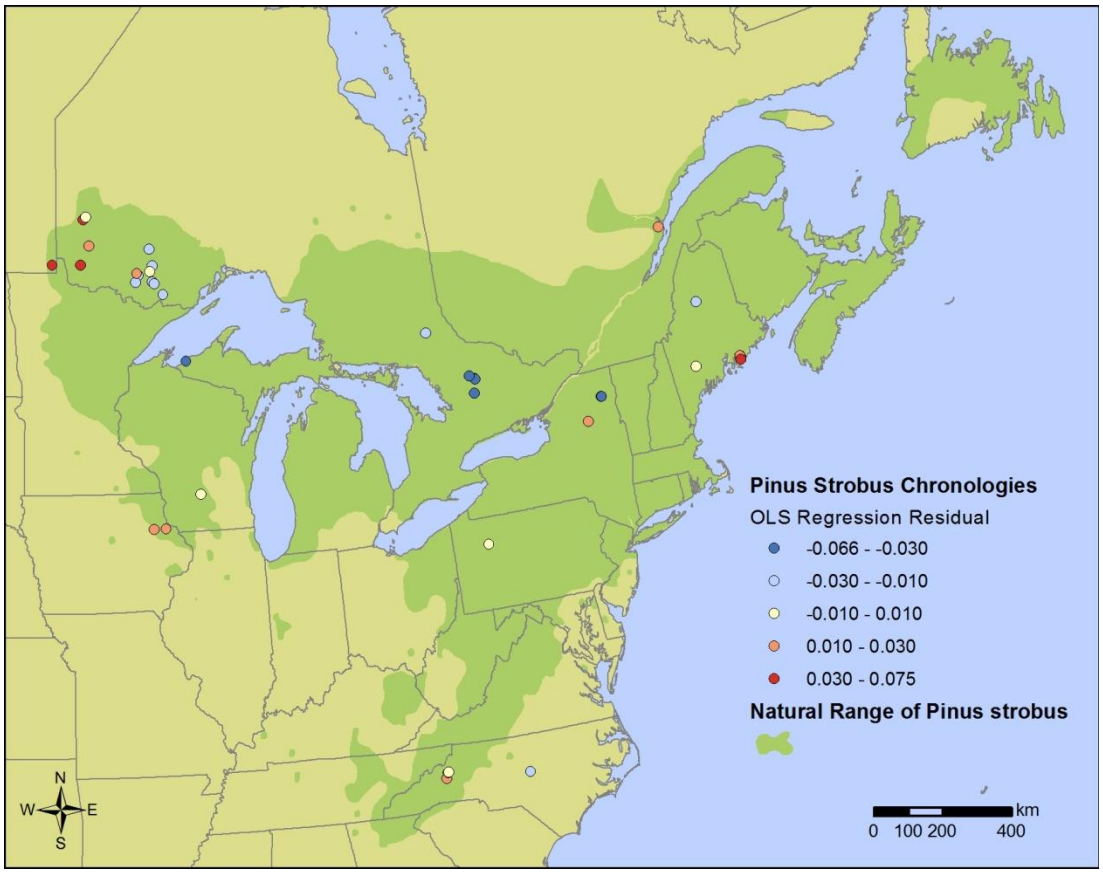

Figure 4.50. Map of residuals from the global OLS regression model.

Geographically Weighted Regression

Since clustering of the global regression residuals was observed within a 400 km distance band, the initial GWR model was run with a fixed kernel bandwidth of 400 km. Even though the resulting model had a much higher R^2 (0.84) and adjusted R^2 (0.77) than that of the global regression, the AICc was also much higher, at −37.2 (versus −150.1 for the global model). Since lower values of AICc are associated with models that are better fit to the data, and since a difference of three or four is seen as sufficient justification for rejecting the model with the higher AICc (Fotheringham et al., 2002), this model was promptly discarded.

Performing a GWR with an adaptive kernel bandwidth that was set to minimize the AICc yielded a much better fit to the observed data. In this case, the AICc was −168.2. The R^2 of this model was 0.65, and the adjusted R^2 was 0.58. The significantly lower AICc (Fotheringham et al., 2002) and the higher R^2 than those found in the global regression indicate that the GWR model was better fit. The adaptive bandwidth selected by the software as minimizing the AICc was that of 31 neighbors, meaning that 84% of the observations were used in the regression equation for each prediction location. The residuals (Figure 4.51) were randomly positioned, according to the Moran's I of −0.02 (p = 0.90).

The fixed kernel bandwidth that minimized the AICc was a distance of 645 km. The model yielded an AICc of −166.4. Since an AICc difference of at least three or four is necessary to select between two models (Fotheringham et al., 2002), the difference of 1.8 between this and the adaptive kernel model was insufficient information to make a determination. The residuals of this model were also randomly distributed (Figure 4.52), with a Moran's I of −0.03 (p = 0.94). The R^2 was 0.69, and the adjusted R^2 was 0.60, so this model was selected for further investigation because of its improved predictive power.

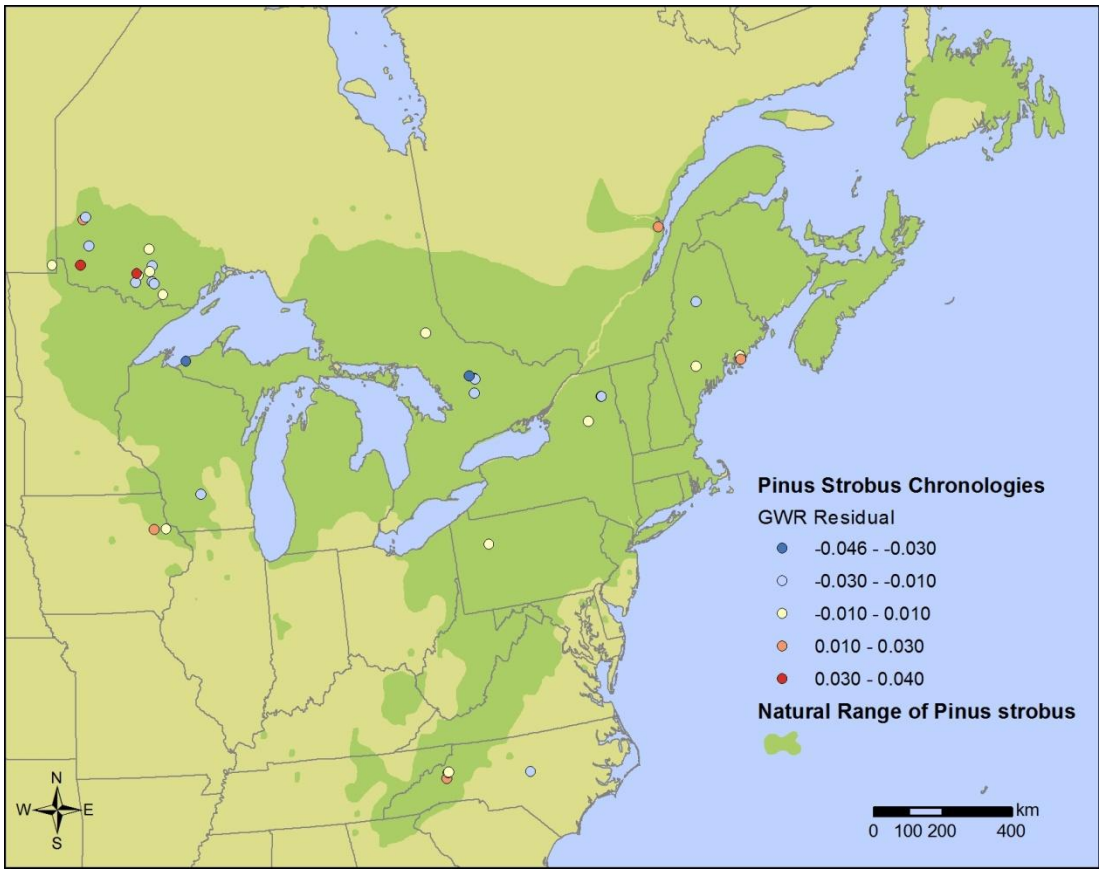

Figure 4.51. Map of residuals from the GWR model with an adaptive kernel bandwidth.

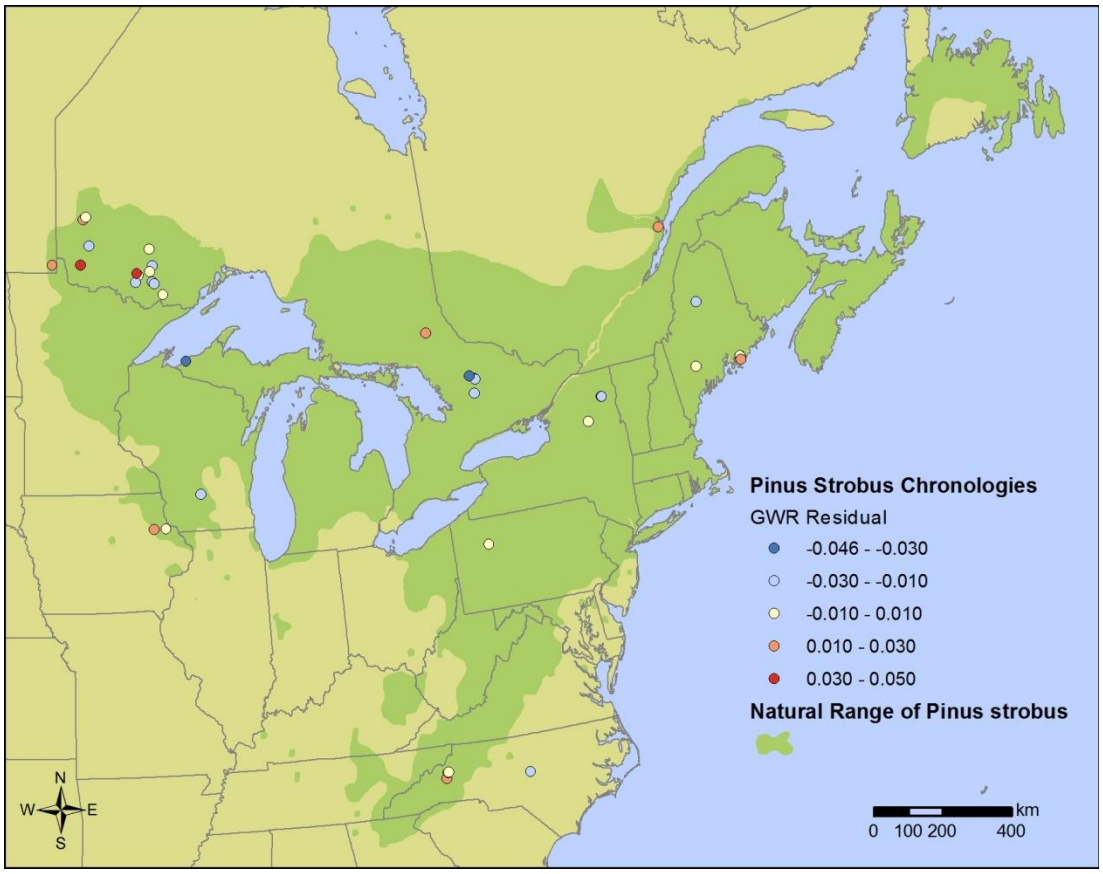

Figure 4.52. Map of residuals from the GWR model with a fixed kernel bandwidth.

Comparison of Figs. 4.13 and 4.16 reveals that the GWR overpredicted mean sensitivity at sites with low observed values and underpredicted mean sensitivity at sites with high observed values. This problem was also present in the global regression model (Figure 4.50). Nevertheless, residuals in the GWR model were lower than those in the global model. The absolute value of residuals in the global model had a mean of 0.024, a standard deviation of 0.017, and a range of 0.001–0.074. For the GWR model, the absolute value of the residuals had a mean of 0.015 and a standard deviation of 0.012, with a range of 0.001–0.050.

A map of the GWR intercept, as it changes across the range of *P. strobus* (Figure 4.53), shows an increasing intercept from east to west. There is also a tendency of intercept values to become more moderate toward the south. This map may be misleading, though, as the software did not estimate coefficients outside the geographical bounds set by the study sites; therefore, the northeastern extent of the estimated coefficients is actually near the center of the species' geographic distribution.

The pattern of change in the precipitation coefficient (Figure 4.54) also has a strong longitudinal gradient, but, in this case, values decrease westward. As with the intercept, these coefficients become more moderate southward. In the northeast of the calculated area, precipitation is positively correlated with mean sensitivity. The coefficients for temperature (Figure 4.55) generally increase from the northeast to the southwest, but the highest values are near the northwestern edge of the range. Only in the northeast are mean sensitivity and temperature inversely related.

The map of predicted mean sensitivity (Figure 4.56) displays a general pattern of increasing values westward. The center of the distribution contains low values, but the lowest values are found at high elevations near the species' southern extent.

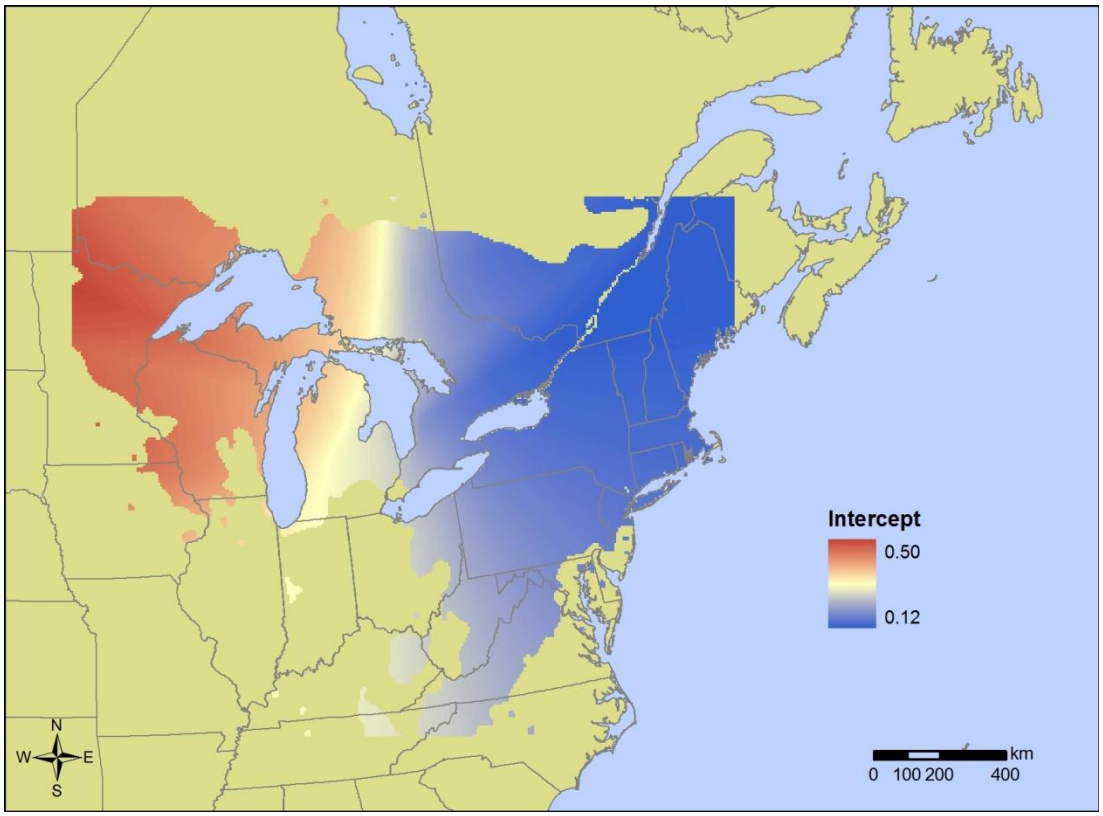

Figure 4.53. Map of intercept, as generated from the GWR model.

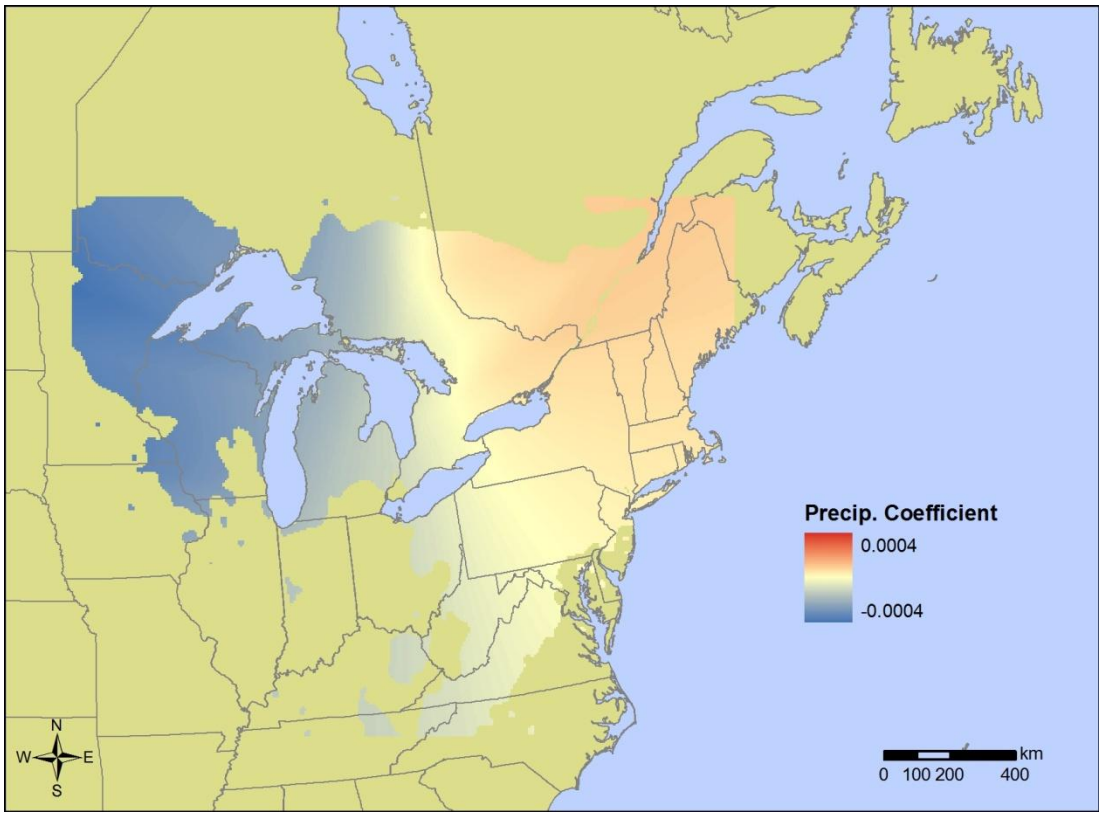

Figure 4.54. Map of the coefficient for precipitation, as generated from the GWR model.

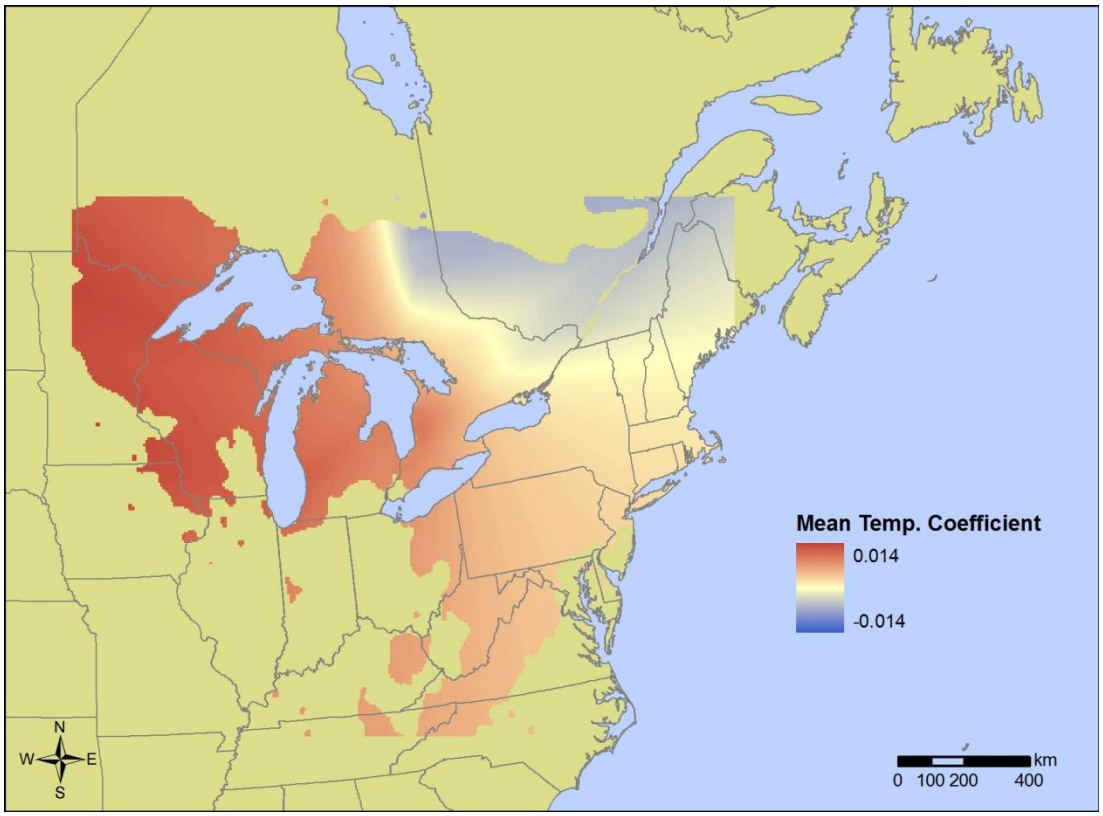

Figure 4.55. Map of the coefficient for temperature, as generated from the GWR model.

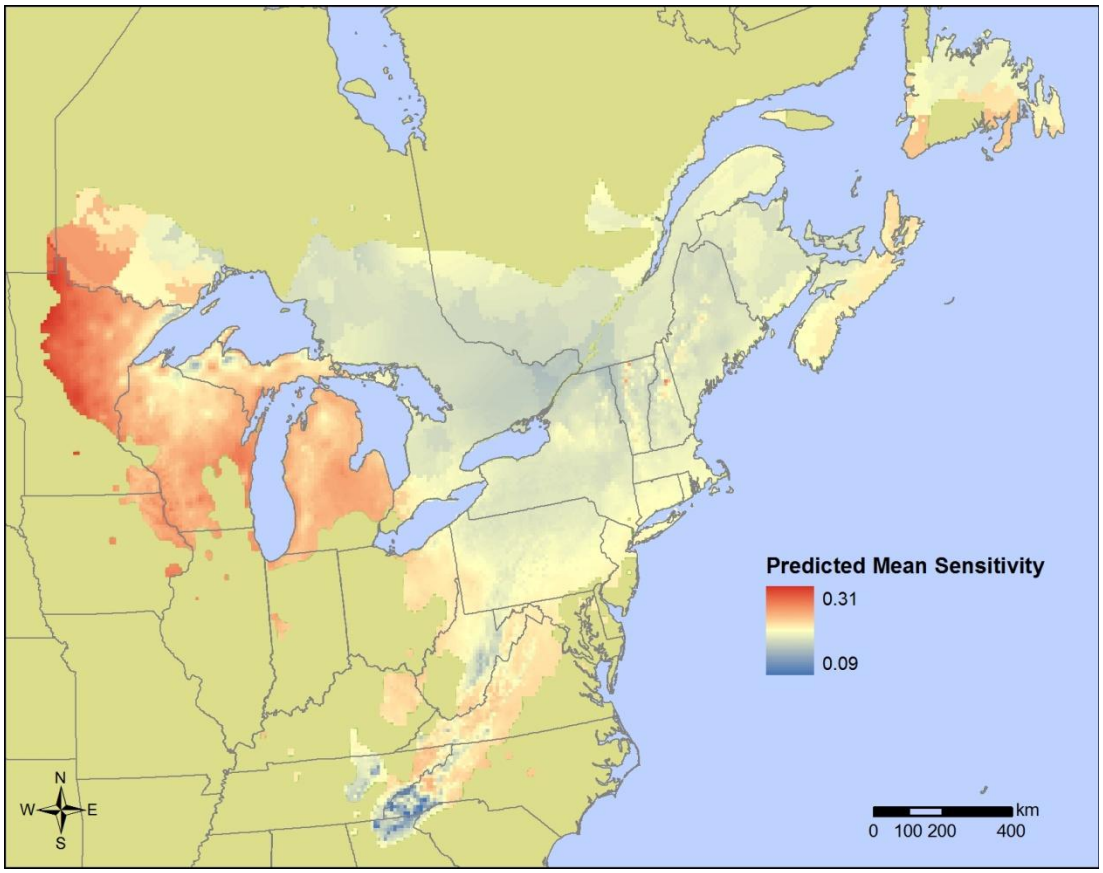

Figure 4.56. Map of predicted mean sensitivity for *P. strobus*.

CHAPTER V

DISCUSSION

Southern Chronologies

Growth Responses

At each of the four sites, warm temperatures in the early spring are associated with wider growth rings. A cooler spring delays the breaking of dormancy, which leads to a shorter growing season (Fritts, 1976). At higher elevations, April temperature becomes more important than March temperature. This is most likely due to later growth initiation at higher, cooler sites.

White Pines Preserve is the only site to demonstrate the growth-limiting role of hot summers. With it being the lowest elevation site, this is unsurprising, as it is the most likely site to experience excessive heat. Hot summers are often capable of reducing growth by increasing the rate of transpiration (Gates, 1965), thereby exacerbating moisture stress and reducing net photosynthesis (Fritts, 1976; Levitt, 1980). Heat can also directly affect the cambium, especially in young trees with thin bark (Levitt, 1980; Jones, 1992; Walker, 1999). A hot summer can lead to reduced growth in the following growing season, as suggested in the results for the White Pines Preserve population. Fritts (1976) explains that reduced net photosynthesis leads to a deficit in energy stores, which are typically accumulated to fuel growth at the beginning of the following season. Fritts (1976) further asserts that even warm winters can deplete energy stores through

moisture stress, since photosynthesis can occur throughout the year in certain conifers. This would explain the negative relationship of growth with previous December temperature at White Pines Preserve.

Radial growth at White Pines Preserve and at the low-elevation site on Linville Mountain is improved by growing season precipitation. During July, which is typically the hottest month, abundant moisture can permit the continuation of efficient photosynthesis and cambial activity (Zahner, 1968; Glerum, 1970). Neither of the two higher elevation sites is limited by growing season precipitation, most likely because of the generally cooler and wetter conditions encountered with increasing elevation. Under such ideal summertime conditions, the atmosphere rarely, if ever, approaches the evaporative threshold that compromises growth. In fact, on Linville Mountain, only growth at the low-elevation site is significantly correlated with any variable in the summer months of the growth year.

Since temperature and precipitation are believed to be most important in their combined effects, one would expect PDSI to be strongly correlated with growth rates. However, PDSI is only correlated with growth at White Pines Preserve, suggesting that the site is more climatically marginal than any of the Linville Mountain sites. This notion is supported by the fact that White Pines Preserve also exhibits stronger responses to temperature and to precipitation than any other site, especially during the summer months.

Temporal Changes

For all three Linville Mountain sites, the moving interval analyses confirm that temperature only makes a noteworthy contribution to growth during the early spring. At the low- and mid-elevation sites, this relationship has been consistent for the past 80 years. The high-elevation site is more complicated. There, early spring temperature no longer seems to influence growth. Instead, warm Novembers have begun to limit growth. At this high of an elevation, the growing season was expected to have already ended by November, so any significant correlation—especially a negative correlation—is confounding. This counterintuitive finding demands further investigation.

For the White Pines Preserve population, the early growing season month during which temperature influences growth has transitioned from March to February. This suggests that growth may be initiating as early as February, or at least that a period of warmth just before the growing season may augment earlywood production. Linear regression of the climate data over time shows that February temperature has increased by over 1˚ C since the year 1895. Current summer temperatures have also recently begun to limit radial growth, but regression reveals that these temperatures have declined slightly over the past 114 years, so this newly developed impact on tree growth may be related to a combination of temperature and moisture. Indeed, regression of the precipitation data indicates that July and August precipitation have decreased by 4.3 and 2.8 cm, respectively, over the observed period.

In the moving interval analyses, precipitation did not present as coherent of a pattern as temperature. Radial increment at each of the Linville Mountain sites was more

highly correlated with antecedent precipitation than with growing season conditions. None of these sites exhibited persistent correlations, and few relationships satisfied the standards of the response function analysis. The increasing relevance of early summer precipitation for growth at White Pines Preserve is probably related to the aforementioned trend of decreasing summer precipitation in that climate zone. This suggests that, though the population formerly received ample rainfall to satisfy growth requirements every year, summer precipitation now occasionally falls below a threshold, beyond which plant function is interrupted. Due to collinearity in the summer precipitation variables, however, this trend was not significant in the response function analysis.

Radial increment at both the mid- and high-elevation sites on Linville Mountain has exhibited negative correlations with PDSI at some time. This has recently become the case from February–June at the mid-elevation site, and it was formerly the case during the summer months at the high-elevation site. One possible explanation is that, since clouds tend to generate the cool, moist conditions that yield high values of PDSI, photosynthesis is retarded by the concomitant low levels of insolation, leading to insufficient energy reserves for fueling growth processes. Just as the calculation of PDSI accounts for a lag effect in moisture conditions, the photosynthetic effects on cambial division may also be lagged (Fritts, 1976). More intuitively, the White Pines Preserve population has shown positive correlations with PDSI during the summer months. Unlike this population's relationships with temperature and precipitation, its response to PDSI has been relatively consistent through the past century.

Mean Sensitivity

Contradicting common assumptions about growth response, local site factors do not seem to have any statistically significant impact on mean sensitivity. In fact, the only arguably significant effect—that of slope at a low resolution—was opposite of the relationship posited by Fritts (1976). At one of the elevation classes in this study, lower values of mean sensitivity were found on steeper slopes. While higher levels of soil moisture—often found on gentler slopes—are capable of interrupting plant function (Kozlowski, 1971; Jones, 1992), this condition has not previously been investigated for its effects on ring-width variability. This omission in the literature is most likely an artifact of dendrochronology's development in the semi-arid southwestern United States, where excess moisture is seldom an issue.

The geographic patterns of mean sensitivity in *P. strobus* confirm the metric's validity in assessments of climatic tolerance. The comparatively low mean sensitivity observed at the disjunct White Pines Preserve population is the only exception to the expected patterns of higher mean sensitivity nearer to range margins. This supports the hypothesis that the genetic isolation of disjunct populations enables them to adapt, whereas their counterparts on the margins of the central population's distribution are limited in their adaptive capacity by gene flow from the range core. The results of Hart et al. (2010) provide further support of this hypothesis. Such disjunct populations, then, may be uniquely rich storehouses of genes for the mitigation of anthropogenic shifts in forest composition (see: Fraser and Bernatchez, 2001; Newton, 2007). An alternate inference is that these disjunct populations fall beyond Fritts' (1966) "forest border",

where mean sensitivity decreases rapidly and ring-width becomes consistently narrow. The strength of correlations between growth and monthly climate at White Pines Preserve—especially when compared to the other North Carolina sites—further supports this latter inference.

The global OLS regression model was able to account for only 21% of the variation in mean sensitivity. The substantial improvement with a GWR model, to explain 69% of the variation, suggests that the relationships of mean sensitivity with precipitation and temperature vary throughout the range of *P. strobus*. The coefficient outputs illustrate the patterns of this variation. The positive relationship between precipitation and mean sensitivity—observed in the far northeastern corner of the output (Figure 4.54)—was unexpected and is quite inexplicable given the current data. Moisture is not known to limit *P. strobus* growth in this region (Fries, 2002), but perhaps the accompanying clouds limit sun exposure. Climate data at a higher temporal resolution could more adequately elucidate the dynamics at work here. The increasing importance of moisture westward is reasonable, given the generally drier conditions in that direction.

Previous authors have stated that the intercept map generated in a GWR can be interpreted as representing the underlying trend in the dependent variable, as it would be without the influence of the independent variables (Huang and Leung, 2002; Işik and Pinarcioğlu, 2006). A model that adequately accounts for variation of the dependent variable should not display any coherent trend or geographic pattern in the intercept. In this case, the obvious trend of an increasing intercept westward (Figure 4.53) implies that mean values of temperature and precipitation do not fully explain mean sensitivity. Some

other variable with a longitudinal trend is at work. One possibility is the annual or diurnal amplitude of temperature. Interior, continental climates experience more drastic shifts in temperature than areas where climate is moderated by large water bodies. Such continentality has been shown to increase values of mean sensitivity (Fürst, 1978). Similarly, perhaps growing season conditions would be more revealing than annual averages.

The negative relationship of temperature and mean sensitivity observed in the northeast (Figure 4.55) is intuitive; at the northern limit of a species, low temperatures should become limiting to growth (Schweingruber et al., 1979; Garfinkle and Brubaker, 1980; Fritts and Swetnam, 1989). However, in the western portion of *P. strobus*' range, the relationship becomes strongly positive, even along the northern range boundary. Given the lower precipitation in this region, high temperatures must exacerbate moisture stress, causing the observed patterns. High temperatures are associated with higher mean sensitivity near the southern extent of the species' range as well, albeit to a lesser degree, as ample moisture tends to be available year-round.

Rather than implying non-stationarity of a linear relationship between mean sensitivity and climate, the patterns evident in the coefficients suggest that the relationship is simply quadratic. Nevertheless, with a more thorough dataset, this method could still be used to define trends in climatic tolerance and even to identify ecotypes of a species. Regardless, this is an effective means of predicting mean sensitivity.

The map of predicted mean sensitivity (Figure 4.56) generally confirms the hypothesized patterns. However, a large region of low predicted values is found at the far southern extent of the species. This initially seems contradictory to the observed patterns, but a familiarity with the local geography clarifies this finding. The region is high in elevation and receives abundant rainfall; therefore, the climate is similar to that of the range center. Perhaps this is why the region is known for producing especially vigorous specimens of *P. strobus* (Johnson, 1995; Smith, 1995).

Contradicting the notion that sensitivity increases toward range boundaries, predicted values of mean sensitivity along the northern margin of *P. strobus*' distribution are low relative to those along the eastern, western, and southern margins. As suggested by DeHayes et al. (2000), *P. strobus*' northern margin may not be related to present climate, but rather to migration lag or to the scarcity of fire, which facilitates establishment. In such a case, climate would not directly constrain radial growth in this region. This also complements the finding of Murphy et al. (2010) that most tree species of eastern North America are better suited to climate in the northern portion of their ranges.

The eastern range margin also tends to display relatively low values of mean sensitivity. This can simply be explained by the fact that the Atlantic Ocean serves as a barrier to establishment and migration. Therefore, this boundary is not climatically-determined, and one should not expect it to conform to the clear patterns of, for example, *P. strobus*' western range margin.

CHAPTER VI

CONCLUSION

Until now dendrochronological studies of *P. strobus* have neglected populations south of Pennsylvania. This omission in the academic literature is especially egregious considering that such populations are likely vulnerable to climatic changes (cf. Jump et al., 2006; Crawford, 2008). This study has expanded the dendrochronological record and further examined the climatic growth response of *P. strobus* across an elevation gradient and at a disjunct site. As suspected, radial increment was most responsive to climate near the species' low-elevation limit and in the disjunct population. This supports the hypothesis that geographically marginal populations are most vulnerable to climate change.

By employing geospatial analysis in the examination of dendrochronological data, this research has brought a novel perspective to the fields of dendroclimatology and population ecology. The observed geographic patterns of mean sensitivity have provided empirical support for Fritts' (1966) conception of the metric as well as for a broader interpretation of it. In spite of long-held assumptions that topographic site factors affect mean sensitivity in ways that compromise broad-scale patterns, statistical analysis shows that neither slope nor aspect has any significant influence on the mean sensitivity of *P. strobus*. The data also suggest that a site's distance from the species' range margin could be an adequate predictor of mean sensitivity. In fact, the correlation of these two

variables, along with a visual examination of Figure 4.49, indicates that this may even be the most relevant factor. However, since elevation, water bodies, migration histories, and land-use patterns can interrupt the distribution of a species and compromise this trend, it is necessary to comprehend the underlying response to climate.

This paper illustrates how a geographically weighted regression is able to quantify the response of mean sensitivity to climate. Whether the relationship of mean sensitivity and climate is non-stationary or simply quadratic is unclear, but similar analysis on a more thorough dataset may be able to discern unique responses and perhaps to distinguish ecotypes, if they exist. Nevertheless, implementing the GWR model has made it possible, not only to estimate the value of mean sensitivity at any location, but to identify the specific climatic variable that limits complacent growth there.

Further analysis of geographic patterns in mean sensitivity should be conducted on other species and in other regions to confirm or to challenge the findings and inferences made here. Also, in future studies, more independent variables should be examined in order to improve the predictive power of the regression models. Specifically, growing season conditions may be more revealing than coarse-resolution, annual data.

Among the practical implications of illuminating geographic patterns for mean sensitivity is an improved method of site selection for dendroclimatic investigations. Researchers have long struggled to adapt traditional dendrochronological site selection criteria to the humid, low-relief landscapes of eastern North America and elsewhere (Cook, 1982; LaMarche, 1982; Phipps, 1982; Speer, 2010). Applying GWR to existing

dendrochronological records can help to locate regions in which sensitivity is high enough to accurately reconstruct climate. Another potential use is the parameterization of spatial variation in the climate-growth relationship into growth/yield models. This would be especially useful for models that intend to consider growth under a changing climate (see: Crookston et al., 2010).

In an era when the natural sciences are focused so intently on forecasting the biosphere's composition over the coming decades, perhaps no work is more critical than deciphering the response of individual species to climate. The assumptions that current distribution represents the fundamental niche and that climatic tolerance is stationary are antiquated and insufficient. The rapid progress of GIS technology has contributed a vast toolbox of accessible analytical techniques, by which existing dendrochronological datasets can be examined in order to better understand the complexities of a species' climatic constraints.

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